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SOME FACTORS INFLUENCING THE EFFICIENCY OF APANTELES MEDICAGINIS MUESEBECK (HYMENOPTERA: BRACONIDAE) AS A PARASITE OF THE ALFALFA CATERPILLAR, COLIAS PHILODICE EURYTHEME BOISDUVAL[1]

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INTRODUCTION

IN CERTAIN of the warmer areas of California, such as the Sacramento and San Joaquin valleys, the alfalfa caterpillar, *Colias philodice eurytheme* Boisduval, causes severe damage to alfalfa. Populations increase rapidly during the summer months, and the caterpillars, if not controlled, may cause complete defoliation of alfalfa fields. In other alfalfa growing areas this pest never becomes abundant.

Two conditions that seem essential for high *Colias* populations are concentrated areas of alfalfa and moderately high summer temperatures such as occur in the San Joaquin Valley. However, within such areas there is always great variation in population density from field to field. There has been some controversy as to whether this variation in *Colias* density is primarily the result of natural enemies, climatic factors, concentrations of alfalfa, or inherent qualities of the *Colias* population.

Floyd (1940)[4] reported the coccinellid *Coleomegilla maculata fuscilabris* (Mulsant) = (*Megilla fuscilabris*) as probably the most important factor controlling the alfalfa caterpillar in Louisiana. Under California conditions, however, it is apparent that such predators are of minor importance. Investigations of the ecology and control of *C. ph. eurytheme* in California (Michelbacher and Smith, 1943; Smith and MacLeod, 1943; Smith and Michelbacher, 1944; Smith and Allen, 1949; and Smith *et al.*, 1949) have shown that the

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braconid parasite, *Apanteles medicaginis* Muesebeck, has a pronounced influence on *Colias* populations. Of the numerous parasites attacking the alfalfa caterpillar, only *A. medicaginis* assumes importance. This small, hymenopterous parasite oviposits inside the early host instars, and the parasite larva completes its development by the time the *Colias* larva reaches the late third or early fourth instar. At maturity the parasite larva emerges from the *Colias*, spins a small, yellowish cocoon, and pupates. The wound inflicted by this emergence causes death of the debilitated host caterpillar in a very short time. Because parasitized caterpillars are killed before reaching the fifth instar, their feeding is greatly reduced. In the case of large populations of *Colias* larvae that have a high level of parasitization, this mortality may at times prevent serious economic damage to the alfalfa.

Another important biotic factor in the control of *Colias* is the polyhedrosis (Thompson and Steinhaus, 1950). This virus disease, in contrast to *A. medicaginis*, does not assume epizoötic proportions until larval populations have become relatively high, and the majority of individuals are in the fourth or fifth instar when killed. Thus, natural control by the virus often takes place after extensive damage to the alfalfa has occurred.

The adult *Colias* prefers to oviposit on short alfalfa shoots, and Smith *et al.* (1949) have explained local variations in *Colias* populations on the basis of concentration of the butterflies at the time of oviposition. However, there are variations in population densities of *Colias* and *Apanteles* which cannot be explained solely on this basis.

The present investigation was undertaken in 1947 to determine some of the more important ecological factors affecting *A. medicaginis*. From the beginning, it was recognized that this parasite is of great value, but since serious economic infestations do occur, there was a need to determine what conditions might have an adverse effect on its efficiency. Information presented here should help in prediction of population densities of *Colias* as well as indicate methods by which the efficiency of the parasite might be increased. Field studies were conducted in the summer, and laboratory work during the remaining months. However, sufficient time was spent in the field during the winter to determine the seasonal history of the parasite. The major portion of the field studies was conducted in the Dos Palos area of the San Joaquin Valley—the type locality of *A. medicaginis*. Material for laboratory studies was also collected from that area.

Many closely interacting factors influence the effectiveness of any parasite. For the sake of convenience and clarity, these factors are dealt with separately in this paper, but no one should be considered as isolated. A parasite may be regarded as effective from an economic standpoint if it is capable of holding the pest population below levels which man considers to be economic. Ecologically, a parasite is effective if it is a major influence in regulating the host population at any level. A parasite may be effective at one time or in one area but not in others. In any case, all the factors of its ecosystem are among those influencing its effectiveness. While all these factors are important, they are not equally so, but vary in significance in different instances. Those factors which appear to be of special significance for *A. medicaginis* are included in the following discussion.

SEASONAL HISTORY OF HOST AND PARASITE

The seasonal history of *Apanteles medicaginis* has been treated previously by Michelbacher and Smith (1943) and by Allen (1958). However, because of its importance in the synchronization of the host and its parasites, a more detailed account of the seasonal history of both is given here.

Table 1 shows the population trends for *Colias* and *Apanteles* during late winter and spring of 1948, in the Westley area of the San Joaquin Valley. *Colias* and *Apanteles* populations were sampled in various alfalfa fields on

TABLE 1

POPULATION TRENDS OF *COLIAS* AND *APANTELES* LARVAE IN ALFALFA FIELDS DURING THE LATE WINTER AND SPRING OF 1948, NEAR WESTLEY, CALIFORNIA

Date	Fields cut once	Fields cut twice	Number of sweeps	Mean number of *Colias* larvae per 1,000 sweeps					
				Small larvae*	I.S.R. larvae†		Medium larvae‡	Large larvae§	Total larvae
					Total	Number with *Apanteles*			
	per cent	*per cent*							
March 4	0.0	0.0	3,050	0.0	15.7	7.3	4.7	2.7	23.1
April 1	0.0	0.0	6,900	0.0	1.2	0.6	1.7	2.9	5.8
April 13	5.0	0.0	3,800	0.0	0.6	0.0	1.3	0.3	2.2
April 27	52.2	0.0	4,350	1.2	0.5	0.2	0.9	0.7	3.3
May 4	67.5	0.0	7,800	0.0	0.5	0.1	0.9	0.1	1.5
May 13	77.5	0.0	8,700	0.4	1.8	0.6	0.5	1.0	3.7
May 25	80.0	2.5	12,800	1.4	5.3	1.3	4.1	1.3	12.1
June 4	82.5	2.5	7,100	0.7	4.4	1.7	5.5	3.4	14.0
June 8	87.5	15.0	5,100	0.6	5.9	2.4	7.6	3.9	18.0
June 18	92.5	60.0	1,400	1.4	10.0	5.0	11.4	2.9	25.7

* Small larvae are less than 5 mm in length.
† I.S.R. larvae are in the size range in which field examination can be made for *Apanteles* larvae. They range from 5 to 11 mm in length, and include late second, third, and small fourth instars.
‡ Medium larvae are fourth and early fifth instar larvae ranging from 12 to 20 mm in length.
§ Large larvae are in the fifth instar, and are over 20 mm in length.

the dates indicated. Each sample was taken by making 100 sweeps with a standard insect net, and usually several positions in each field were sampled. Since temperatures at Westley during January and February are too low for any appreciable development of either insect, the data for March 4 represent the overwintering population. Numerous winter surveys in other areas and other years substantiate the conclusion that this is a typical overwintering population. Although a few individuals of both *Colias* and *Apanteles* might have emerged prior to March 4, the bulk of the population remained in the larval stage. Parasitism of the overwintering population was relatively high. Of all the larvae collected, about 50 per cent of those which could be evaluated for parasitism were parasitized. The amount of parasitism varied from field to field, but both parasitized and unparasitized larvae were well distributed throughout the fields that were sampled. There was no correlation between host density and the degree of parasitism at this time.

During the latter part of March and first half of April, development accelerated, many *Colias* pupated, and consequently the larval population decreased. By April 13, only 5 per cent of the fields had been cut, but the larval population had declined greatly as a result of pupation. Since it was not until April 27 that 50 per cent of the fields were cut, it is reasonable to assume that many of these individuals were able to complete their de-

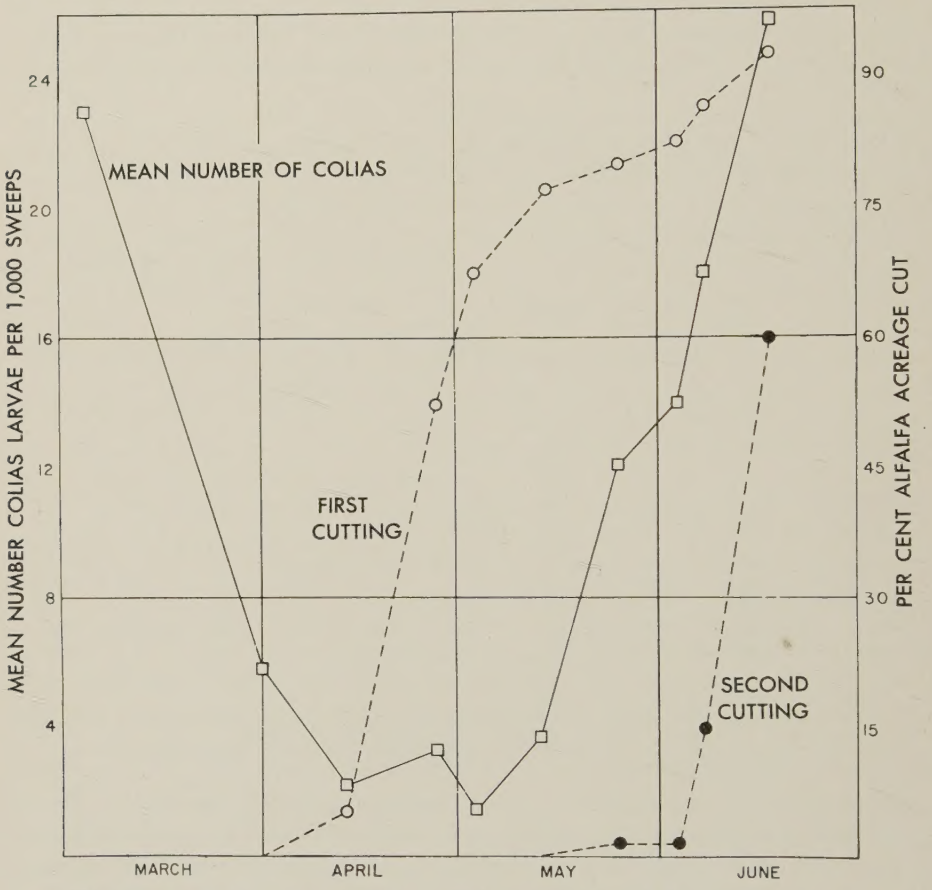

Fig. 1. Relation of *Colias philodice eurytheme* larval populations to cuttings of alfalfa in the Westley district.

velopment and emerge as butterflies. A large proportion of the larvae and pupae, still present at the time of cutting, was undoubtedly destroyed. The first cutting terminates larval development and emergence for most of the overwintering *Colias* population in alfalfa.

The growth period for the second cutting of alfalfa in the Westley area extended from the latter part of April to the middle of June (table 1). It is during this period that the first spring brood of *Colias* develops. Larval populations, although low, show a steady increase during this time. The increase in the *Colias* collected was partly the result of large larvae being

easier to collect by sweeping, but also resulted from a prolonged oviposition period. Development of both *Colias* and *Apanteles* was poorly synchronized with alfalfa culture at this time. The larval population trend increased rapidly during the first half of June, but over 50 per cent of the fields were then cut for the second time. Since the bulk of the second brood was still in the larval stage at the time of cutting, most of the individuals were kept from completing their development (fig. 1). Although April and May were cooler than normal in 1948, the population trend of *Colias* and the lack of synchrony with the second cutting of alfalfa are typical for the first brood of *Colias*. In warmer springs the second cutting would occur in late May or early June.

The degree of parasitism of this first spring brood was moderately high—about 20 to 40 per cent—even though *Colias* populations in this and the preceding generation were relatively low. This degree of parasitism, at low host densities, suggests that *A. medicaginis* has very good searching ability, for only a limited number of females could have emerged from the small overwintering populations that were present in the fields.

Michelbacher and Smith (1943) studied the population trends of *Colias* from June through November in the Tracy-Patterson area of the San Joaquin Valley and in the San Francisco Bay area. These workers found that, in the cooler San Francisco Bay area, populations of *Colias* remained at a low level throughout the year, and the proportion parasitized by *Apanteles* was relatively large. In the San Joaquin Valley, the second brood of *Colias* generally occurs in June although in cool years, such as 1942 and 1948, it may be retarded so that it extends from the middle of June to the middle of July. This second brood is considerably larger than the preceding one, and its development is much more closely synchronized with the cutting cycle. Parasitism of the second brood is generally comparable with that of the spring generation.

The third brood, which occurs in July and August, often results in the first economic infestations. Populations are usually much higher than in the preceding brood, and development of *Colias* is well synchronized with the cutting cycle. Parasitism at this time is somewhat higher than in the second brood, but is still generally below 60 per cent in most of the fields.

The fourth brood, which occurs in August and September, represents the highest population of the year. Parasitism at this time is relatively high—often 90 to 95 per cent of the larval populations in many of the fields. It is during this time that potentially economic infestations are often rendered sub-economic by the parasite.

The fifth brood, which occurs in late September, October, and November, is much smaller than the fourth brood, and only rarely are fields economically infested. This decrease in the population densities seems to result from a combination of factors. Parasitism alone, although high during this brood, does not account for the sudden decrease. Much lower temperatures during this period undoubtedly help bring about the decline by retarding development, but there seem to be undetermined biotic factors which also contribute to this decline.

The more advanced individuals of the fifth brood probably emerge and

start a partial sixth brood, but it seems likely that it is primarily the fifth brood which is overtaken by cold weather, and hence passes through the winter. The proportions of the overwintering population arising from these two broods are determined by how far development has advanced when cold weather sets in.

SYNCHRONIZATION OF HOST AND PARASITE

To be effective, a parasite must be synchronized with its host so that susceptible stages of the host are present at the same time that adult parasite females become mature. To help determine how well *Colias* and *Apanteles* developmental periods could be synchronized, a study was conducted to

TABLE 2

RATE OF *COLIAS* DEVELOPMENT AT VARIOUS CONSTANT TEMPERATURES

Temperature	Number of insects	Number completing development*	Developmental period (days)							
			Egg		Larva		Pupa		Total	
			Range	Mean	Range	Mean	Range	Mean	Range	Mean
deg. C		*per cent*								
35	45	4.4	2.0– 3.0	2.5	11–13	11.9	3– 4	3.9	18–20	18.3
32	10	80.0	2.5– 3.5	2.8	9–13	10.4	4– 5	4.4	17–21	17.5
30	33	36.4	2.5– 3.0	2.9	9–13	10.9	4– 5	4.9	17–21	18.7
25	15	66.7	3.5– 4.5	4.0	16–18	16.9	6– 8	6.9	27–28	27.7
20	15	60.0	6.0– 9.0	6.7	27–34	30.5	11–12	11.7	46–51	48.9
15	37	29.7	13.0–16.0	15.0	48–65	56.4	23–32	27.3	86–110	98.7

* Mortality resulted mainly from polyhedrosis, except at 35° C. where there was a direct adverse effect of temperature.

discover the rates of development of the two at various constant temperatures. During the course of this study it was found that parasitism influences the time required for development of *Colias* instars, and the larval instar of *Colias,* which is parasitized, influences the time required for larval development of *Apanteles.* In addition to these interactions in the development of host and parasite it was found that, at low temperatures, the developmental rate of *Colias* is reduced, so that the time between cuttings of alfalfa precludes development of *Colias* within the time of one crop period.

The rearing procedures used in this study were similar to those described for *Apanteles medicaginis* (Allen, 1958). However, when *Colias* were to be reared to adults it was found necessary to place the pupae in small screen cages so that the adults could expand their wings after eclosion.

Effect of Temperature on Colias. Nonparasitized *Colias philodice eurytheme* were reared at temperatures ranging from 15° to 35° C. The development times of the different stages are shown in table 2. Although polyhedrosis caused a moderate mortality at all temperatures, it was clearly evident that 35° C was unfavorable, for only two out of 45 individuals completed development at that temperature. This high mortality occurred mainly at the time of the molts. Often the head capsule of the previous instar

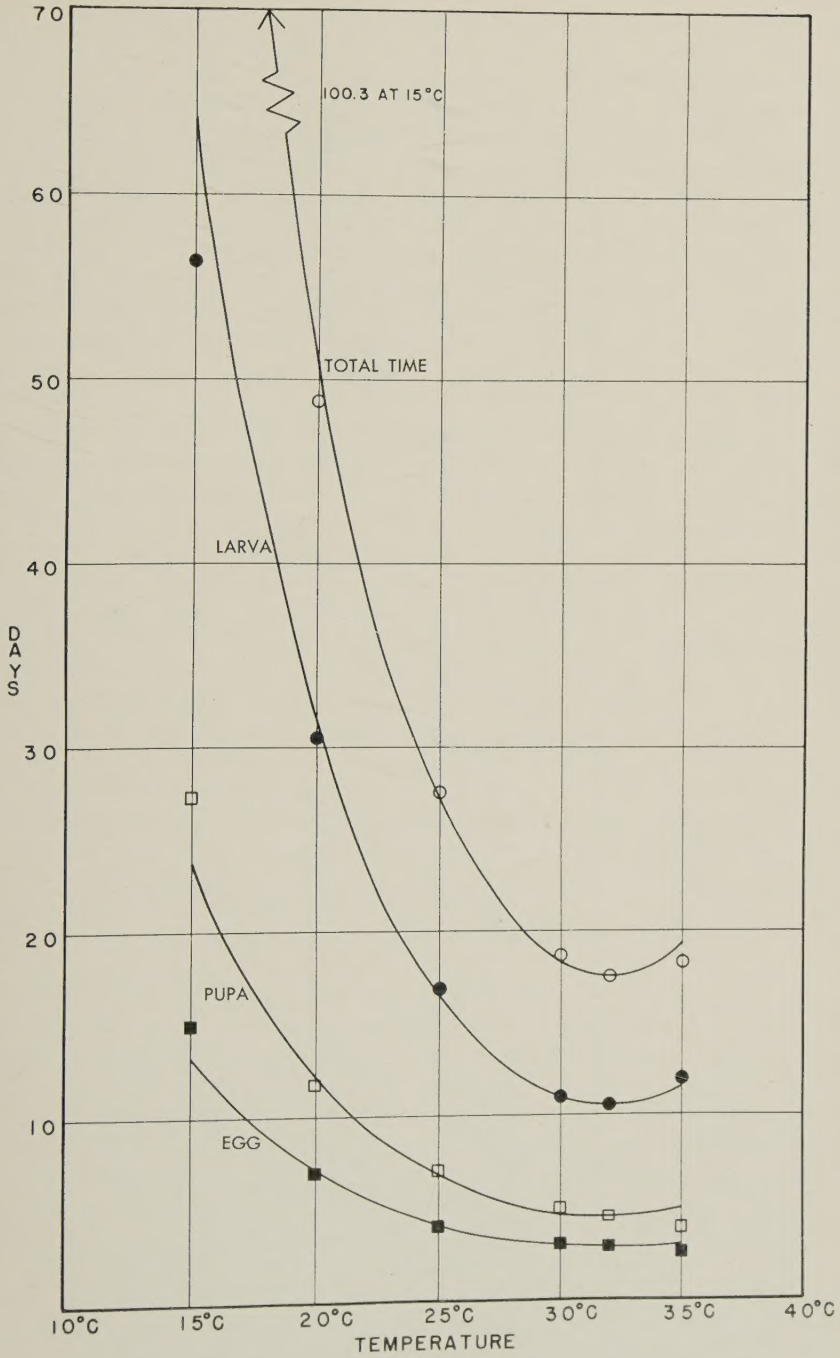

Fig. 2. Time-temperature curves for development of the various stages of *Colias philodice eurytheme*.

TABLE 3

RATE OF *COLIAS* LARVAL DEVELOPMENT AT VARIOUS CONSTANT TEMPERATURES

Temperature	Number of insects completing development	Developmental period (days)													
		First instar		Second instar		Third instar		Fourth instar		Fifth instar		Prepupa		Total	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
deg. C															
35	4	2– 3	2.4	1– 5	1.9	1– 3	2.0	2– 3	2.2	2– 3	2.8	0–1	0.6	11–13	11.9
32	8	2– 2	2.0	2– 3	2.1	1– 3	1.8	1– 2	1.6	2– 3	2.1	0–1	0.8	9–13	10.4
30	12	2– 3	2.2	1– 2	1.8	1– 2	1.7	1– 3	1.9	2– 4	3.0	0–1	0.3	9–13	10.9
25	10	3– 5	3.6	2– 4	2.9	2– 3	2.2	2– 4	3.0	4– 5	4.4	0–1	0.8	16–18	16.9
20	9	5– 8	6.6	4– 6	4.5	3– 7	4.7	5–11	6.8	6– 8	6.7	0–2	1.3	27–34	30.5
15	11	9–16	11.9	6–12	8.4	8–11	9.4	8–14	10.2	11–19	13.4	3–3	3.0	48–65	56.4

remained over the newly formed head, resulting in considerable distortion and, finally, death from starvation.

The optimum rate of development seemed to take place at about 32° C. Both total development and larval development were most rapid at that temperature, and although data for the eggs and pupae were slightly shorter at 35° C, the differences were not significant. The minimum development time for *Colias* of about 17.5 days, as determined by this study, agrees very closely with the time determined by Michelbacher and Smith (1943).

The data in table 2 are shown in graphic form in figure 2. Mean times of development at the various temperatures are presented as dots and squares. The curves were calculated by means of Janisch's catenary (Janisch, 1925, 1932; Huffaker, 1944). The formula for this catenary may be expressed as $t = \frac{m}{2}(a^T + a^{-T})$ where t = time, m = developmental time at the temperature giving the optimum rate of development, T is the temperature in degrees centigrade above or below this optimum, and a is a calculated constant which determines the slope of the curve. For *Colias* the values of a were calculated to be 1.141 for the egg stage, 1.159 for the larval stage, 1.149 for the pupal stage, and 1.154 for total development from egg to adult. The values of m were 2.8 days for the egg stage, 10.4 days for the larval stage, 4.4 days for the pupal stage, and 17.5 days for total development.

Development at 15° C was comparatively slow, the egg stage requiring 15 days, the larval stage 56.4 days, and the pupal stage 27.3 days. Hence total development from egg to adult required about 98.7 days. By extension of the curve (fig. 2), it appears that the threshold of development should be very close to 12.5° C.

In table 3, larval development is divided into the time of development for each instar. There is some variation in the proportion of the total time required for each instar at different temperatures. Some of these differences can be explained by the fact that cultures were examined only once a day, and the time of development for each instar is rather short. At the lower temperatures, the times for each instar are longer, hence the relative differences can be more clearly seen.

These laboratory data are useful in interpreting population phenomena that may be encountered under field conditions. Although it is well known that naturally fluctuating temperatures may have a somewhat different effect on development, reproduction, and mortality than do artificially constant temperatures, it appears to us that such effects are not large enough to influence seriously the inferences that can be drawn as to the limiting effects of temperature and cutting on *Colias*. A greater difficulty in the correlation of laboratory and field data is the lack of information on the temperature conditions prevailing in the microenvironment of the *Colias*. Fortunately, recent studies permit certain generalizations to be made.

The plant growth of the alfalfa crop has an ameliorating influence on the temperatures in the *Colias* microenvironment as compared with those of the general environment or the environment of the standard weather-instrument shelter. The extremes are reduced and the mean temperature is two or three degrees warmer in the alfalfa. On the other hand, when a field is

harvested the conditions in the *Colias* microenvironment are acute. In summer, the maximum temperatures in the stubble may exceed those from standard instrument shelters by 20° C or more.

The periodical harvesting of the alfalfa crop has a drastic impact on the *Colias* physical environment. As indicated above, the *Colias* population is suddenly plunged from the ameliorated conditions before cutting into lethal physical conditions. Furthermore, the larvae are also exposed to the predation of birds and insects such as *Calosoma*. It is critical therefore, that the *Colias* larvae complete their development before the field is cut. The temperatures prevailing in the alfalfa canopy must be high enough to permit this.

The second cutting period in most alfalfa growing areas of northern California is 35 to 45 days. During the active growing season the alfalfa is usually cut every 28 to 40 days. From figure 2 it can be seen that conditions comparable with those of constant temperatures of 21° C or higher would be necessary if *Colias* development were to be completed in 40 days or less, and similarly, temperatures above 24° C would be necessary if development were to be completed in 30 days. Since an alfalfa field remains in a stubble condition unfavorable for oviposition for several days or more after cutting, relatively high temperatures would be necessary for *Colias* to complete their development within the growing period of a single cutting of alfalfa.

Examination of temperature records for microenvironment stations in central California indicates that there is a good correlation between temperatures and *Colias* infestations. In the San Francisco Bay area where *Colias* is never a pest, the highest monthly mean temperature is considerably less than 20° C, and throughout the rest of the summer conditions are cooler. Under such conditions *Colias* would require more than 60 days to complete their development, which is far longer than the period for a single cutting of alfalfa. In the San Joaquin Valley, on the other hand, the monthly mean temperature in the alfalfa is above 25° C in both July and August, and is above 22° C from June through September. Under these conditions, development could be completed in from 28 to 33 days—within the normal cutting period of the alfalfa. General observations over many years in the Dos Palos area and elsewhere confirm this conclusion. In the San Joaquin Valley the emergence of butterflies from an alfalfa field is closely timed to the cutting. In fields where the cutting is made earlier than normal, the emergence of butterflies is greatly reduced. In fields where the cutting is delayed, a very large proportion of the brood emerges and may seriously aggravate the general infestation of the area.

From the laboratory data it is also apparent that temperatures above 35° C have an unfavorable influence on *Colias*. Areas highly favorable for *Colias*, such as the western portion of the San Joaquin Valley, often have maximum temperatures above 35° C, but the *Colias* larvae can survive in areas with such high temperature because the ameliorating effects of the alfalfa growth protect them from the extremes. On the other hand, when the alfalfa is cut under such conditions the caterpillars are immediately exposed to lethal temperatures. A few can survive on plant growth at the

margin of the fields and on stems missed by the mowers. It seems likely that only limited areas, such as the low deserts of California, have temperatures sufficiently high in the alfalfa canopy to affect *Colias* populations adversely.

It would appear that in many areas, temperature plays a very significant role in limiting the abundance of *Colias*. At the lower temperatures, *Colias* development is retarded and does not coincide with the cutting cycle of alfalfa. In such situations, when the alfalfa is harvested the larvae are exposed to unfavorable physical conditions, they are made more vulnerable to predators, and their food supply is reduced. At the high temperatures, there is an adverse effect on *Colias* development, and at the time of cutting,

TABLE 4

RATE OF *APANTELES MEDICAGINIS* DEVELOPMENT AT VARIOUS CONSTANT TEMPERATURES

Temperature	Number of insects	Number completing development*	Developmental period (days)						Total‡
			In *Colias*		In cocoon		Total†		
			Range	Mean	Range	Mean	Range	Mean	
deg. C		*per cent*							
35	64	6.25	6–10	6.9	3– 4	3.8	10–10	10.0	10.6
32	17	70.59	6– 7	6.5	3– 5	4.0	10–12	10.5	10.5
30	41	41.46	6– 8	6.8	3– 5	3.9	9–13	10.5	10.6
26.7	42	69.05	7–12	8.3	4– 6	4.5	11–16	12.9	12.8
25	26	65.39	8–11	9.3	5– 8	5.5	13–17	14.7	14.9
20	49	38.78	13–19	16.0	8–11	9.4	21–30	25.3	25.3
15	46	41.30	24–34	28.2	16–20	17.8	40–55	46.0	46.0

* Mortality resulted mainly from polyhedrosis, except at 35° C, where there was a direct adverse effect of temperature.
† Based on individuals completing development.
‡ Based on summation of mean time in larval host and mean time in cocoon.

severe, direct lethal effects. Depending on the conditions prevailing in a particular field, these lethal actions may affect the population in a density-dependent manner. When the *Colias* populations are high, the available places in which the larvae can survive (uncut alfalfa stems, marginal plants, etc.) are limited. Hence, the higher the populations of larvae, the higher will be the percentage which does not survive. Needless to say, other factors, such as *Apanteles*, continue to influence *Colias* populations under these conditions, but unfavorable temperature is a critical factor which precludes population increase and contributes directly to mortality.

Effect of Temperature on Apanteles. The average times of development of *A. medicaginis* at temperatures ranging from 15° to 35° C are summarized in table 4. In nearly all cases the host caterpillars were in the late first instar when parasitized; hence, these developmental times are somewhat shorter than for parasites in which oviposition had occurred in the early first instar (table 5).

As with *Colias*, at 35° C there was a very high mortality both within the host caterpillar and in the cocoon. Although mortality was always high as a result of polyhedrosis of the host caterpillars, it was much higher at 35° C

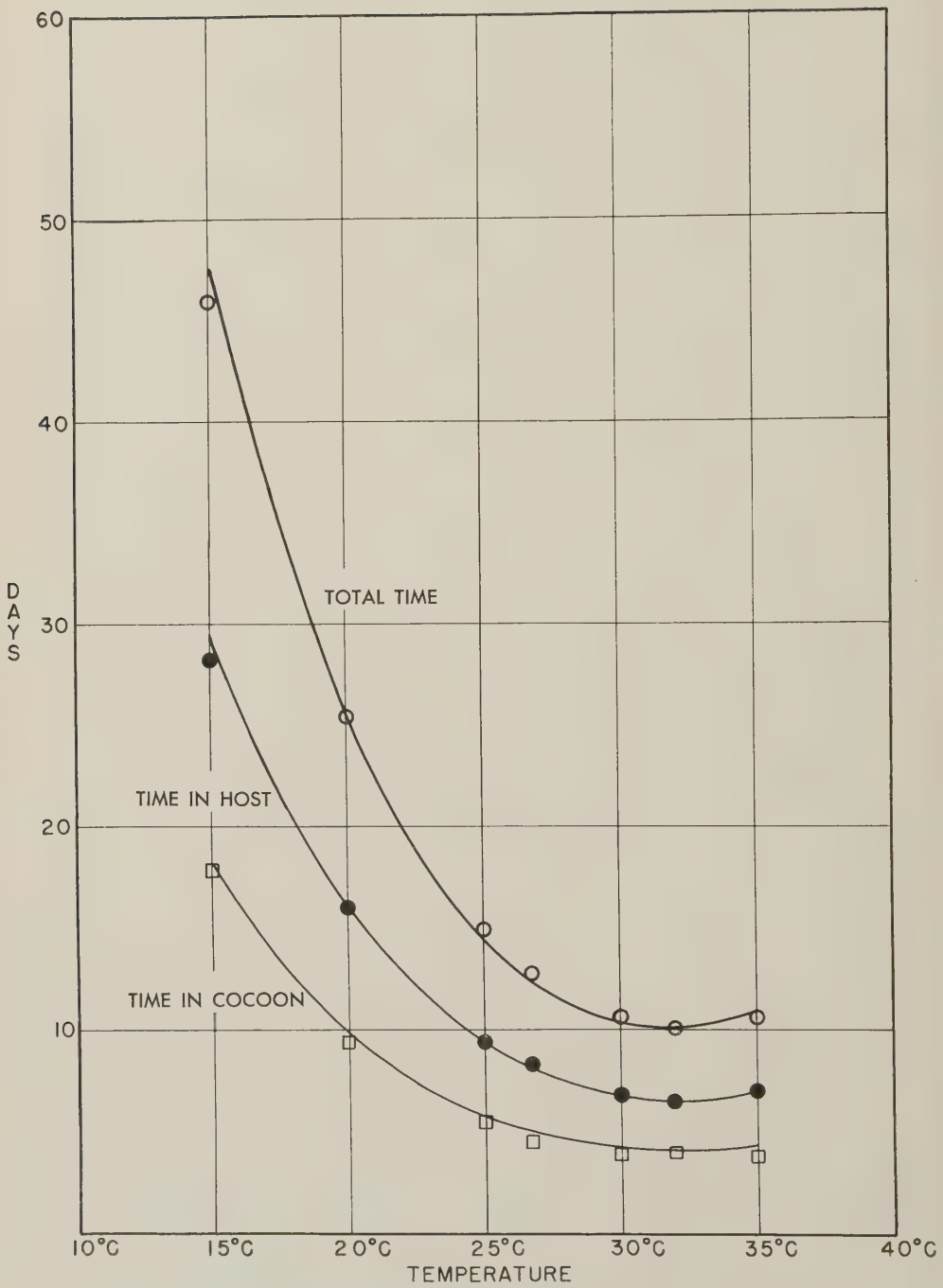

Fig. 3. Time-temperature curves for development of the various stages of *Apanteles medicaginis*.

because of the adverse effect of high temperature. Dissections revealed that, in many cases, the parasite larvae within the caterpillars had died and had subsequently been incapsulated. At this temperature only 25 out of 64 individuals emerged from the host caterpillars, and of these 25, only four completed pupation. Because of the high mortality in the cocoon stage, there is a relatively large discrepancy between the total time of development based on the four individuals that completed development and the total time calculated by the summation of average times for the two stages.

The data in table 4 are graphically presented in figure 3. As with the graph for *Colias* development, the curves were drawn according to Janisch's catenary. For *Apanteles* the values of a were calculated to be 1.138 for the time in the host, 1.138 for the time in the cocoon, and 1.141 for total development. As with *Colias,* the maximum rate of development was obtained at about 32° C. The values for m (minimum times of development) used in calculating the catenary were 6.5 days for the time in the host, 4 days for the time in the cocoon, and 10 days for total development.

At 15° C, the lowest temperature at which rearings were conducted, development within the host caterpillar required 28.2 days, and the time spent in the cocoon was 17.8 days. Continuation of the developmental curve (fig. 3) indicates that 12.5° C would be the approximate threshold temperature as was the case with *Colias.*

At most temperatures, the development of *Colias* from egg to adult requires about twice the amount of time that *Apanteles* does (fig. 4), but at temperatures below 19° C, the data show that *Colias* requires more than twice the time. Although this small difference may be real, a very small difference in rearing temperature may have caused the slight change in ratio.

Effect of Alfalfa Culture and Colias Oviposition. The much shorter time of development for *Apanteles* would be a greater advantage if it were not for the peculiar habitat which alfalfa provides. *Colias* females lay most of their eggs in alfalfa fields which have recently been cut and have just started to grow (Smith, *et al.*, 1949). For this reason the *Colias* are all in about the same stage of growth at any one time in a particular field. When adequate moisture is available to the alfalfa plant, the new shoots appear rapidly after cutting. At that time the growth is very attractive to female *Colias,* and the major part of oviposition takes place. This stage of attractiveness lasts for about a week, and then oviposition in the field is greatly reduced. Oviposition preference for young growth by the adult *Colias* is an important feature which allows *Colias* to be a pest on alfalfa, for eggs laid later in the growth of the crop are rarely able to develop to pupation before the next cutting.

This limited period of oviposition results in a restriction of the parasitizable stages (first, second, and third instars) to an approximate period of only two weeks. That is, oviposition is spread over one week and development from the first instar through the third instar requires another week at 26.7° C. At that temperature, *Apanteles* requires 13 days for development. Thus it can be seen that very few would be able to complete a second generation in the same field. Only the progeny from the very first

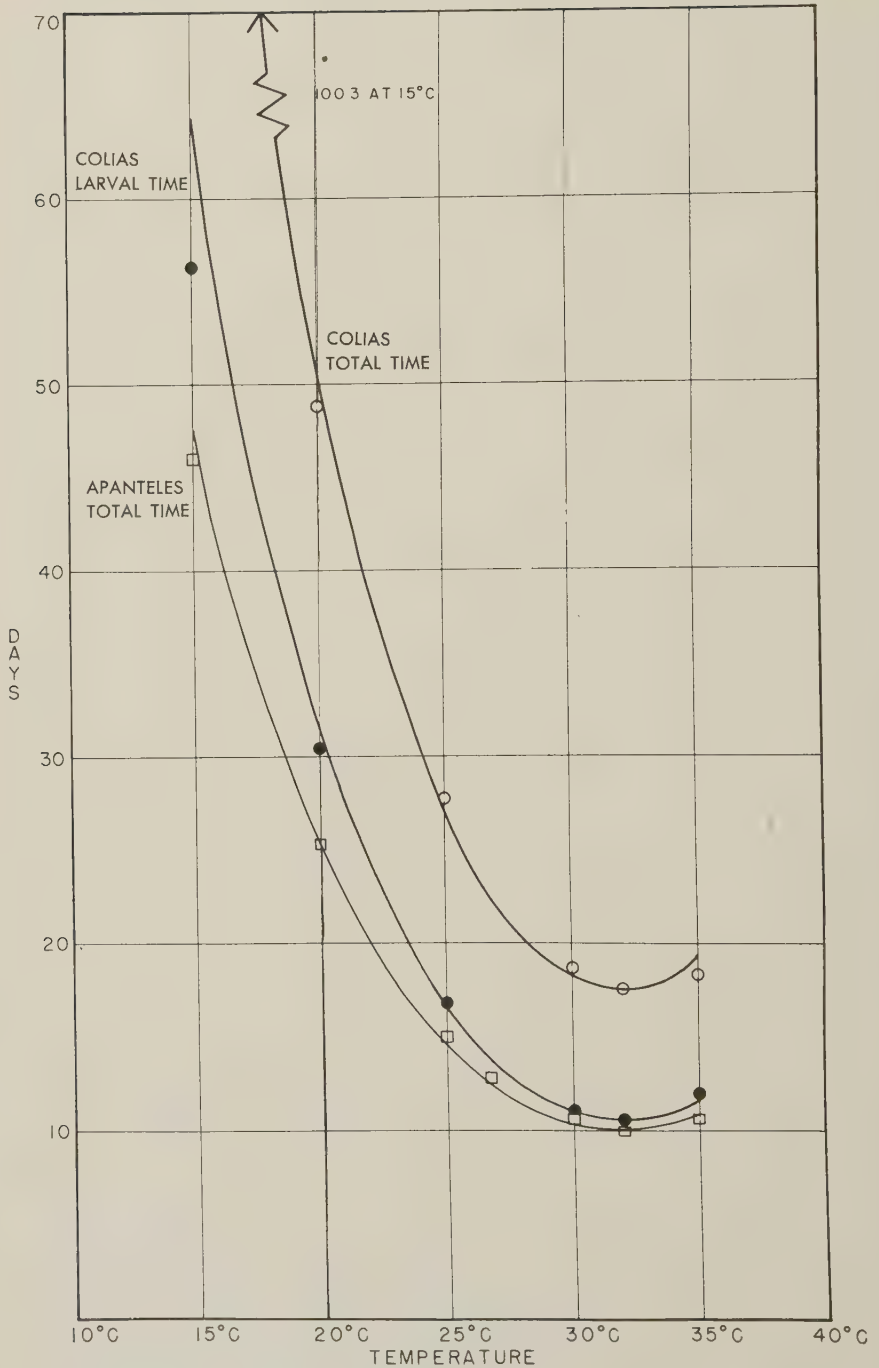

Fig. 4. Comparison of time-temperature curves for *Apanteles medicaginis* and *Colias philodice eurytheme*.

ovipositions would find suitable hosts upon emergence, and these larvae would only be suitable for oviposition for a very short time.

Thus, in an alfalfa field with a cutting cycle of 30 days, under ideal conditions the earliest *Apanteles* adults would emerge on about the fourteenth day. These would issue from *Colias* hosts that had developed from eggs laid on the first day after cutting and had hatched in the minimum incubation time of two and one-half days. Such early adults of *Apanteles* might still have time to produce a second generation before the next cutting, but very few hosts of suitable size would still be available, and they would remain suitable for parasitism for only a few days. In most situations, the emergence of the earliest *Apanteles* adults is considerably later, because suitable host larvae are not usually available until about seven or more days after a field has been cut.

TABLE 5

DIFFERENTIAL RATE OF DEVELOPMENT OF *APANTELES MEDICAGINIS* AT 26.7° C WHEN OVIPOSITION OCCURS AT DIFFERENT TIMES IN THE EARLY INSTARS OF *COLIAS*

Development of *Colias* when parasitized	Number of insects	Developmental period (days)					
		In *Colias*		In cocoon		Total	
		Range	Mean	Range	Mean	Range	Mean
Early first instar	17	8–14	10.1	4–6	5.1	12–20	15.1
Late first instar	9	7–10	8.2	4–5	4.4	12–15	12.7
Second instar	16	7– 9	7.7	4–6	4.8	11–14	12.5

Before alfalfa was cultivated, *Colias* was dependent on native legumes. These varied in abundance and location both yearly and seasonally, resulting in population changes of *Colias*. However, these vegetational changes were undoubtedly not so abrupt as those produced by the cutting of alfalfa. Under such conditions, the more rapid rate of development of *Apanteles* would allow it to respond much more rapidly to changes in host density than is the case in the alfalfa habitat.

Effect of Parasitism on Colias Development, and Influence of Host Size on Apanteles Development. A parasite within a host larva may bring about several changes in the host before killing it. For example, codling moth larvae parasitized by *Ascogaster quadridentata* Wesmael are only one-fourth to one-third normal size (Clausen, 1940). Larvae of *Pseudaletia unipuncta* (Haworth) parasitized by *Apanteles militaris* (Walsh) eat less than half as much as do unparasitized larvae (Tower, 1916). Larvae of the oriental fruit moth, *Grapholitha molesta* Busck, are retarded in their development when parasitized by *Macrocentrus ancylivorus* Rohwer (Haeussler, 1932). On the other hand, the host affects the development of the parasite. Johansson (1951) pointed out that *Apanteles glomeratus* (Linnaeus) development was retarded by small hosts or by overcrowding within the host. For *Apanteles medicaginis* there is a difference in the time of development when parasitization takes place in the early first, late first, and second instar larvae of

Colias (Michelbacher and Smith, 1943). From table 5 it can be seen that the time spent within the host caterpillar is longer when the early first instar caterpillar is parasitized, whereas there is little difference between the late first and second instar.

The time of development for second, third, and fourth instar *Colias,* both parasitized and unparasitized (table 6), shows that development of the second instar is only slightly retarded by parasitism. The duration of the third instar prior to emergence of the parasite is prolonged considerably when the parasite emerges from the third instar, but when emergence is from the fourth instar, the third instar seems to be of almost normal duration. When

TABLE 6

MEAN DEVELOPMENTAL PERIOD OF PARASITIZED AND UNPARASITIZED *COLIAS* LARVAE AT VARIOUS CONSTANT TEMPERATURES

Temperature	Developmental period (days)						
	Second instar		Third instar			Fourth instar	
	Unparasitized	Parasitized	Unparasitized	Parasitized*	Parasitized†	Unparasitized	Parasitized
deg. C							
35	1.9	1.7	2.1	2.0	3.8	2.2	2.2
32	2.1	1.8	1.8	1.7	3.2	1.6	2.0
30	1.8	2.2	1.7	...	3.5	1.9	...
26.7	2.4	3.0	2.0	2.3	4.2	2.2	2.5
25	2.9	3.5	2.2	3.0	4.5	3.0	3.0
20	4.5	5.7	4.7	4.0	8.1	6.8	5.0
15	8.4	10.2	9.4	9.7	15.7	10.2	9.0

* *Apanteles* emerging from fourth instar.
† *Apanteles* emerging from third instar.

emergence is from the fourth instar, the time spent by the parasite in this instar is about equal to the time for complete development of the unparasitized fourth instar. In spite of these compartively equal growth times, however, development of the fourth instar *Colias* is negligible, and actual growth is considerably retarded.

An important aspect of this retardation of growth by parasitism, not directly concerning synchronization, is its effect on the evaluation of parasitism. Because of this retardation, parasitism in a population should be calculated on the basis of larvae of an equal age rather than of an equal size. From table 5 it can be seen that at 26.7° C *Apanteles* development within *Colias,* when parasitization takes place in the early first instar, requires about 10 days and, as pointed out by Michelbacher and Smith (1943), emergence is from the third instar. Nonparasitized *Colias* under the same conditions during this period of time would develop through the fourth instar. Likewise, when parasitization takes place in the late first or second instar, *Apanteles* development requires eight days, and emergence is from the fourth instar. Nonparasitized *Colias* of an equal age develop into the early fifth instar during this same length of time.

Since early first instar *Colias* are preferred by *Apanteles*, it would seem advisable to calculate the percentage parasitism of a population by determining the number of parasites in a given number of third- and fourth-instar *Colias*. Michelbacher and Smith (1943) calculated the percentage of parasitism by determining the number of parasites present in *Colias* larvae of such size that the parasite larvae could easily be detected with the naked eye. This size range was from 5 to 11 mm in length, and included late second-, third- and small fourth-instar *Colias*. Within this size range, the number of hard-to-detect, first-stage larvae is generally negligible. Since this size range selected for sampling is the same for parasitized and nonparasitized larvae, it is obvious that the longer time spent in this size range by parasitized *Colias* larvae tends to give an erroneously high percentage of parasitism. Roughly calculated from table 6, parasitized larvae remain in this size range for five days at 26.7° C, whereas nonparasitized caterpillars remain in this size range for only three days.

From the differential rates of development of parasitized and unparasitized caterpillars it can be seen that, at the time the major portion of the *Apanteles* population has reached the cocoon stage, the *Colias* are in the fifth instar. *Apanteles* adults emerge at about the time that *Colias* are pupating, for the time of development of the parasite within the cocoon is approximately equal to the time required for *Colias* to complete the fifth instar and prepupal stage. The *Apanteles* adults must therefore wait a considerable period until progeny from the *Colias* of that generation are available. This period includes the time spent by the *Colias* in the pupa, the preoviposition period, and the incubation period of the eggs. The minimum time required for development of the pupa and incubation of the egg at 32° C is about six and one-half days, while at 26.7° C the time is about nine days. To this time must be added the preoviposition period for *Colias*, determined by Stern (1952) to be about two days. Consequently, a period of eight to 11 days elapses between emergence of *Apanteles* adults and the hatching of eggs from butterflies arising from the *Colias* population that developed in the same field.

Although certain assumptions must be made concerning the relative effects of constant and fluctuating temperatures, it would appear that, in any particular field, *Apanteles* is rarely able to complete a second generation within a cutting period. Hence, the *Apanteles* adults must move from the field of origin. Under conditions undisturbed by man, it is undoubtedly an advantage for *Apanteles* to develop more rapidly than *Colias*, but this leads to complications where *Apanteles* and *Colias* are developing under the conditions existing in cultivated alfalfa. If adjacent fields contain large numbers of suitable hosts, *Apanteles* is not harmfully affected by this lack of synchrony. However, because of the cyclical nature of *Colias* infestations in alfalfa fields, *Apanteles* populations frequently must wait a considerable time until large numbers of suitable *Colias* larvae become available. Any such delay is a disadvantage to the *Apanteles* population. The factors affecting the synchrony of *Apanteles*, *Colias*, and the growth of alfalfa undoubtedly have an important influence on the relative effectiveness of this parasite from one field to another.

LONGEVITY OF ADULT APANTELES

Longevity of adults can be a very important factor in determining the efficiency of a parasite. The area that a parasite can search and the number of eggs laid are both influenced by longevity. In addition, adults that live a short time must have their development synchronized with that of their hosts if susceptible stages of the host are to be available when parasite adults are present. For *Apanteles,* the importance of adult longevity was demonstrated in the previous section where it was shown that the adults must either find suitable hosts in adjacent fields or wait some time until they become available in the same field.

Materials and Methods. Preliminary tests with 50-mesh, brass screen cages with petri dish tops and bottoms proved unsatisfactory for longevity studies. Although food was available and the cages were kept in the dark,

TABLE 7

LONGEVITY OF ADULT *APANTELES MEDICAGINIS* AS AFFECTED BY HUMIDITY AT 21 ± 2° C

Relative humidity	Males			Females		
	Number of insects	Range	Mean	Number of insects	Range	Mean
		days	*days*		*days*	*days*
100	31	3–17	10.6	22	1–22	13.8
92	26	4–22	13.2	26	1–23	14.9
76	30	3–33	16.3	17	5–30	17.1
60	36	9–42	22.2	27	4–35	23.8
55	45	6–43	24.1	12	15–46	28.2
44	29	10–36	22.8	28	13–44	22.7
30	39	3–48	18.6	13	6–29	18.4

the adults lived an average of only 9.5 days. Subsequent work showed that pint ice cream cartons with gauze tops and bottoms were more suitable for the maintenance of adults. Water was provided in a ½-dram vial with a gauze-covered cotton plug. These vials were inserted, plug down, through a hole in the gauze top of the cages. Food in the form of raisins, honey, and "MRT" (protein hydrolysate [Hagen, 1950]) was placed on the end of a toothpick in such a manner that the other end could be inserted in the water-containing vial. It was recognized that the water may have produced a humid microhabitat within the cage. However, it was felt that, at humidities below the hygroscopic point of honey (55 per cent relative humidity), a lack of available food would overshadow the effect of humidity unless a suitable water source were provided to moisten the honey. Food and water were changed every two or three days in order to avoid fermentation and the growth of mold.

Adults for these tests were obtained by collecting both parasite cocoons and parasitized *Colias* larvae in the field and holding them in the laboratory until the parasite adults emerged. The emerging adults were removed daily

and divided at random into lots of about 20 individuals. These groups were then placed under the experimental conditions. Random segregation of the adults was facilitated by working in a cold room at a temperature of 2.2° C for a short period of time. In all experiments the dead adults were removed daily and tabulated according to their sex.

Experiments on the effect of humidity on longevity were conducted by placing gauze-covered cages in glass desiccators that were partially filled with various saturated salt solutions. The relative humidities inside the desiccators were tested frequently by means of a Serdex type HGS-HY-1 hygrometer. The desiccators were all held in the dark at a temperature of approximately 21° C. Since all of the humidities were tested at the same time, other conditions were identical. The relative humidities tested were: 100, 92, 76, 60, 55, 44, and 30 per cent.

Effect of Humidity. Longevity reached its maximum at 55 per cent relative humidity (table 7), and decreased sharply at humidity levels above and below that value. The average longevity for the three replicates at 55 per cent relative humidity was 24.1 days for males and 28.2 days for females. The maximum longevity for one female was 46 days. At 100 per cent relative humidity the averages of three replicates were 10.6 and 13.8 days for males and females, respectively, and at 30 per cent the averages were 18.6 and 18.4 days, respectively.

Longevity varied considerably, depending on the source of the adults and the date of emergence. The adults collected as cocoons lived longer than did those collected in parasitized larvae from another field. In addition, the adults from the first field, that emerged on the last day, lived a shorter time than did those that emerged on the preceding days. The reasons for these differences are not known, and because of this variation the ranges in longevity reported in table 7 are large. Nevertheless, the relative values at each humidity are the same for all the adults, and for this reason considerable stress can be placed on the effect of humidity.

Females appear to live longer than males, but the differences between the two are not marked. The females emerging on any one day lived longer than the corresponding males that emerged on the same day, but because of the variability of the results it is impossible to determine longevity exactly for either males or females.

Effect of Food, Water, and Light. Experiments on the effect of food, water, and light show even more clearly the difficulties involved in studies on longevity of this insect. Conditions were similar to those in the previous experiment except that the cages were not kept in desiccators, but were exposed to a room temperature 22 ± 3° C and a relative humidity of 65 to 75 per cent.

The adults, including those provided with food, lived a much shorter time than did those in the humidity tests (table 8). In those experiments, the average longevity for three replications at 76 per cent relative humidity was 16.3 days for males and 17.1 days for females, whereas in this experiment the average longevity for six replications was 9.3 days for males and 11.3 days for females. The reasons for these differences are not known. Despite this decreased longevity of adults provided with food, it is apparent

that food is a very critical factor, for adults deprived of food lived an average of only 2.5 days (table 8). The availability of water had little or no effect in the absence of food. Although several replications were run in both the light and dark, longevity could be prolonged only slightly in the dark, and in all the tests without food the maximum longevity obtained was only 5 days. Numerous workers (Crossman, 1922; Vance, 1931; Parker, 1935) have mentioned that longevity is greatly prolonged by maintaining the

TABLE 8

AVERAGE LONGEVITY OF ADULT *APANTELES MEDICAGINIS AS* AFFECTED BY PRESENCE OR ABSENCE OF FOOD AND WATER

Sex	Food and water present			Water only			No food or water		
	Number	Range	Mean	Number	Range	Mean	Number	Range	Mean
		days	*days*		*days*	*days*		*days*	*days*
Males	69	2–23	9.3	86	1–5	2.5	75	1–5	2.2
Females	75	3–30	11.3	86	1–4	2.6	62	1–4	2.2

adults in the dark. Although it seems probable that adults kept in the dark would be less active and hence would live somewhat longer, there was not a pronounced difference in longevity when *A. medicaginis* was exposed to light.

Factors Affecting Longevity Under Field Conditions.—Prior to the experiments on longevity, it was thought that humidity conditions might be important in determining the efficiency of *A. medicaginis*, for entomologists working in the Dos Palos area had noted that fields adjacent to the San Joaquin River often have much more parasitism than those farther out on the western plain of the valley. In addition, the work of Michelbacher and Smith (1943) showed clearly that parasitism was very high in the humid San Francisco Bay area even though the population density of the host was very low. However, investigation of the humidity of alfalfa fields, coupled with laboratory data, indicates that humidity is not the critical factor. Data obtained from numerous fields indicate that the humidity does not vary in a way that can be correlated with the abundance of *A. medicaginis*. Although stubble fields are critically dry, all fields which have appreciable growth seem to have a humidity suitable for *A. medicaginis*.

Food supply, shown to be a very critical factor in the laboratory, affords a much more plausible answer to the higher parasitism that is found along the San Joaquin River and in other areas. Observations made in the field showed that adult *Apanteles* feed on nectar from numerous plants, and on honeydew excreted by aphids. Adults have been found feeding on the nectar of morning glory (*Convolvulus arvensis* L.), sunflower (*Helianthus annuus* L.), and silversheath knotweed (*Polygonum argyrocoleon* Steudel). They were also found feeding on honeydew excreted by *Chaitophorus* sp. on willow and *Rhopalosiphum maidis* Fitch on Johnsongrass (*Holcus halepensis* L.).

At the time of these field studies, no insect that produced significant amounts of honeydew during the summer months was feeding in abundance

on alfalfa. Recently, the establishment of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), in California alfalfa fields has greatly modified this situation. Speculations on the significance of the large amounts of honeydew produced by this aphid can be made, but the problem has not been investigated.

In areas of California where *Colias* is a serious pest, alfalfa is grown in large fields which are relatively pure stands with very few weeds. Since alfalfa flowers do not seem to be a satisfactory food source, it is evident that *Apanteles* must find food in some other habitat. A similar dependence of a parasite on nectar and honeydew has been reported for several species of *Typhia* (Clausen, 1940). In areas where alfalfa is grown over extensive acreages and there are relatively few weeds between the fields, very little food is available for *Apanteles* adults. Under such conditions, it seems likely that the limited food supply is a critical factor limiting the efficiency of the parasite.

In addition to nectar-producing flowers, Johnsongrass infested with aphids appears to be an important source of food for *Apanteles*. Because the aphids are generally situated far down in the developing leaf sheaths, the *Apanteles* feeding on the honeydew are not very evident, but the widespread abundance of this weed in and around certain alfalfa-growing areas suggests that it is an important source of food.

Since the plants that provide food are much more common on the margins of fields, it would appear that small, irregularly shaped fields would insure the best feeding opportunity for *Apanteles* adults. Such a dependence on more than one vegetational type has been reported for many tsetse flies, especially *Glossina morsitans* (Swynnerton, 1940). This species is dependent on savanna woodland for rest and breeding, but must have adjacent vleis (temporary marshes) to provide food for the adults.

The higher parasitism in fields along the San Joaquin River may very well result from the greater availability of food for *A. medicaginis* and the consequent greater longevity of the adults. Fields in this area tend to be smaller than usual in size, and irregular in shape. Vegetation is therefore abundant on their margins, and they contain many weeds.

It has been pointed out that low temperature acting directly on *Colias* is a significant contributing factor for low populations in the San Francisco Bay area; it seems that *A. medicaginis* may also have a greater longevity in this area. The work of Michelbacher and Smith (1943) shows that the percentage of parasitism is relatively high even though host populations are very low. Fields in this area are small, weedy, and have exceptionally diverse surrounding vegetation. It is probable that these conditions are favorable for *Apanteles* adult survival, and thus help make possible the parasitizing of a high percentage of *Colias* in spite of extremely low host populations.

This discussion has suggested reasons why *A. medicaginis* may be less efficient in areas where alfalfa is grown in large acreages and little other vegetation is present. Although such conditions may exist in areas where *C. philodice eurytheme* assumes its greatest importance as a pest, it is not necessarily true that the decreased efficiency of *A. medicaginis* is the only

or most important factor causing these high populations. It is possible that, rather than any decreased effectiveness of the parasite, other conditions in the environment are favorable and permit *Colias* populations to increase to high levels in these areas.

REPRODUCTIVE CAPACITY

The total number of eggs a female is capable of laying is another important factor determining the ability of a parasite to overtake or to reduce host populations. In many instances, *Colias* populations increase so rapidly in

TABLE 9

NUMBER OF EGGS PRODUCED BY INDIVIDUALS OF *APANTELES MEDICAGINIS*

Oviposition	Number of days	Total eggs laid	Mean number of eggs per day	Eggs remaining in ovarioles	Total number of eggs
hours/day					
1	5	61	12.2	130	191
1	5	106	21.5	97	203
1	5	74	14.8	103	177
1	6	32	5.3	127	159
1	6	51	8.5	114	165
1	7	33	4.7	106	139
1	11	107	9.7	80	187
1	7	58	8.3	117	175
1	5	25	5.0	101	126
1	18	225	12.5	71	296
1	4	50	12.5	80	130
7	5	80	16.0	74	154
7	10	155	15.5	83	238
7	11	161	14.6	91	252
Mean	7.5	87	11.5	98.1	185

individual fields that the *Apanteles* adults present are unable to maintain their original level of parasitism. A high reproductive capacity is important for a parasite which moves from field to field after each generation, for concentration of the host does not necessarily mean that the parasite will also be concentrated in the same field. This separation of host and parasite populations seems to be of common occurrence with *A. medicaginis* and *C. philodice eurytheme* because of the cutting cycle of alfalfa and the different flight ranges of the two species.

There is no published information concerning the reproductive capacity of *A. medicaginis,* although Flanders (1942) mentions egg storage in the genus *Apanteles* and presents an illustration of the reproductive system of *A. medicaginis.* He makes no mention of the number of eggs that this species can store.

Dissection of 47 females which had been used in the experiments on longevity showed that the oviducts contained an average of 81.6 eggs, with a maximum of 141 and a minimum of 30. On the other hand, female *Colias* have been found to lay more than 1,000 eggs at times, and under favorable

conditions, average more than 100 eggs per female (Stern, 1952). Because of this large difference in reproductive capacities, further experiments were conducted to determine the number of eggs laid by *A. medicaginis*.

Newly emerged females were placed in cages similar to those used in the longevity experiments, and the adults were fed in a similar manner. The cages were maintained in the dark except at the time when host larvae were presented to the females, and kept at room temperature (21 ± 2° C) and 65 ± 5 per cent relative humidity. The first 11 females (table 9) were left with host larvae for one hour each day, and the last three females were left with host larvae for seven hours each day. About 10 larvae were exposed to each female each day, and thus, because of superparasitism, there were nearly always some larvae that were not parasitized. After exposure to the parasites, the *Colias* larvae were either dissected immediately, and the eggs counted, or they were held at a low temperature until dissections could be made. By this procedure the eggs were kept from hatching; hence, no larvae were present to destroy the surplus eggs.

As can be seen in table 9, the number of eggs laid was very low as contrasted with *Colias*, and did not increase much when host larvae were available for seven hours rather than for one. The low number of eggs per day, combined with the short longevity of the adults, resulted in a very small total of eggs laid. The average longevity of 7.5 days was very short, considering that most of the females were from the same stock that, in the humidity experiments, lived for 17.1 days. However, this 7.5 days is not too different from the results in other longevity experiments. The average number of eggs laid per day was 11.5, and the maximum was 21.5 The total number of eggs laid averaged 87, and the maximum was 225. The latter, comparatively large number of eggs were from a female that lived 18 days—much longer than the average. Even in this case, the female laid only 12.5 eggs per day. Dissection of females after death revealed that in no instance was all the supply of eggs depleted.

This reproductive capacity is low as compared with that found for several other species of *Apanteles*. The ovaries of a gravid female of *A. glomeratus* may contain over 2,000 eggs (Clausen, 1940), and Crossman (1922) estimated the reproductive capacity of *A. melanoscelus* to be about 1,000 under field conditions. This latter estimate was based on a laboratory maximum of 535 eggs. Parker (1935) obtained an average of 402 eggs from five *A. solitarius* Ratzeburg, and Vance (1931) found that the ovaries of *A. thompsoni* Lyle contained an average of 230 eggs.

Although it is impossible to state how many eggs *Apanteles medicaginis* is capable of laying, because of the inconsistent longevity, it does seem quite evident that this parasite does not lay many eggs per day. *Colias philodice eurytheme*, on the other hand, lays numerous eggs (50 to 100 per day). Even assuming a longevity of 30 days, which was obtained only under the most favorable conditions, the *Apanteles* females would lay only about 450 eggs at a rate of 15 per day. From the other data available, this seems a high estimate. Since available information indicates that *C. ph. eurytheme* lays considerably more eggs than this, it is highly probable that, if *A. medicaginis* had a higher reproductive capacity, it would be a more effective parasite

in those situations in the summer months when *Colias* populations increase rapidly.

Under natural conditions in which *Apanteles* could complete two generations for each one of *Colias*, this lower reproductive capacity would probably be of little consequence. It takes on special significance, however, when alfalfa fields are cut. Not only is *Apanteles* limited to one generation for each generation of its host, but also limited numbers of *Apanteles* females often encounter large numbers of *Colias* larvae after butterflies have been concentrated in certain fields.

SUPERPARASITISM

Superparasitism is the deposition within a host, by a single parasite species, of more eggs than can complete development. In the case of gregarious parasites, the number of individuals that can develop within a single host is usually determined by the food and space available. Solitary parasites,

TABLE 10

SUPERPARASITISM BY INDIVIDUAL *APANTELES MEDICAGINIS* WHEN OFFERED 10 HOSTS IN A CONFINED SPACE

Number of parasite eggs per host	0	1	2	3	4	5	6	7	8	over 8
Frequency	435	379	177	78	36	10	4	2	2	0

on the other hand, may be limited by food or space, but in many cases the surplus individuals are killed by direct internecine action (Fiske, 1910).

If *A. medicaginis* is like other solitary *Apanteles* studied, it lays but a single egg when it oviposits in its host. When *A. medicaginis* is confined with numerous caterpillars in the laboratory, it apparently oviposits with little or no selection for unparasitized larvae. During the studies on total oviposition, individual females were confined daily with about 10 host larvae. Subsequently, the larvae were dissected and the number of eggs in each recorded. These data (table 10) did not fit a Poisson distribution, a fact suggesting that there was some reason for oviposition not being strictly at random. However, the differences between the two distributions did not indicate that unparasitized individuals had a greater chance of being parasitized, but, on the contrary, showed that certain larvae were parasitized more than might be expected by chance alone. This suggests that certain larvae were either more attractive or were in such a position that they were encountered more often by the parasites. Under laboratory conditions, there was no indication that ovipositing females showed any discrimination between parasitized and unparasitized larvae. Since there was a high frequency of unparasitized larvae in this study, it is evident that superparasitism did not result because unparasitized larvae were not available.

Since *Apanteles medicaginis* adults will readily oviposit more than once in a host, the question arises as to why only one parasite develops in each host. Numerous dissections showed that mortality did not occur in the egg stage, but that elimination of the surplus individuals took place while the

Apanteles were first-instar larvae, so that only one individual progressed to the second stage. Numerous dead, first-stage *Apanteles* could be found in superparasitized caterpillars, and in one case a first-stage *Apanteles* was found with its mandibles piercing another living, first-stage larva. From this it is strongly suggested that internecine action disposes of the surplus individuals in superparasitized caterpillars as was reported for *Apanteles angaleti* Muesebeck by Narayan *et al.* (1956).

Since superparasitism was a common occurrence in the laboratory, an investigation was made to determine the amount of superparasitism in nature. This proved difficult because the surplus individuals are immediately attacked after hatching of the first egg, and the probability of encountering superparasitism is low unless the amount of parasitism is very high. First-

TABLE 11

SUPERPARASITISM BY *APANTELES MEDICAGINIS* UNDER FIELD CONDITIONS

Colias instar	Field	Number of larvae	Unparasitized larvae	Parasitized larvae	
				One *Apanteles*	More than one *Apanteles*
First	A	33	16	17	0
First	B	3	1	1	1
Second	A	31	5	25	1

and second-instar *Colias* were collected in fields which had high populations of adult *Apanteles*. Because superparasitism is evident only a short time after hatching of the first *Apanteles*, the caterpillars were maintained at low temperatures until dissections could be made in the laboratory. This was done by placing the caterpillars in pint-sized ice cream cartons in a portable ice box.

The percentage of superparasitized individuals was very low (table 11). In contrast to the results found in the laboratory, there does not seem to be a high degree of superparasitism in nature. Field A had a very high *Colias* larval population, and *Apanteles* adults were abundant. Fifty sweeps over the alfalfa yielded 21 adult females; 20 sweeps in the alfalfa yielded eight parasitized caterpillars and 15 first- and second-instar *Colias*. Since these small caterpillars are not readily obtained in a net, the 15 individuals represented a very high population which was expressed 13 days later by a population of 160 parasitized and 70 nonparasitized larvae in 20 sweeps. In this field the percentage of parasitized larvae was high, but only one caterpillar was found superparasitized with two first-instar *Apanteles*. In field B, *Apanteles* adults were very common, but *Colias* larvae were so scarce that an adequate sample could not be obtained. In this sample two out of three were parasitized and one of these contained five first-stage *Apanteles* larvae and one egg. In this case it is possible that the *Apanteles* females had built up oviposition pressure because of their high ratio to *Colias* larvae.

It can be seen that superparasitism occurs in nature, but not to the extent that it can be demonstrated under the artificial conditions of the laboratory.

This indicates that *Apanteles* do not oviposit at random, but discriminate between parasitized and unparasitized caterpillars in the field. This discrepancy between the laboratory and field data is probably caused by the crowded conditions in which the females were held in the laboratory.

Several field workers have also found that, on very rare occasions, two or even three second-stage *Apanteles* larvae may be present in a single host larva. Although many thousands of dissections were made in the course of this study, the condition was found on only two or three occasions. It would seem that, in those cases, the *Apanteles* larvae never came in contact with each other until they were second-stage larvae and no longer had functional mandibles. Since more than two individuals never emerge from a single host, it is probable that lack of food or space eliminates one before emergence.

It has been suggested that, in fields with very high adult *Apanteles* populations, *Colias* larvae might be killed by numerous oviposition wounds. Both laboratory and field data tend to indicate that mortality of *Colias* from such wounds is very rare. Superparasitism may at times be common in the field, but *Colias* larvae show a considerable tolerance to oviposition wounds. Laboratory work indicates that a *Colias* larva can withstand repeated oviposition by *Apanteles*. This evidence, plus rarity of fields with such extremely high ratios of parasite adults to host larvae, indicates that mortality from superparasitism is not an important factor in the control of *Colias*.

SEX RATIO

Apanteles medicaginis has arrhenotokous ovaries. The haploid eggs develop into males if not fertilized, and into females if fertilized. This type of reproduction is found in many Hymenoptera and most *Apanteles*. One exception in the genus *Apanteles* is *A. thompsoni* Lyle which has thelyotokous ovaries (Vance, 1931). In this species, only diploid eggs are produced, and they all develop into females.

Since unfertilized eggs develop into males, and fertilized eggs develop into females, the progeny of unmated females will be all males. In addition, the sex ratio of a mated female will depend on the proportion of the eggs fertilized at the time of oviposition. Flanders (1946) reviewed the control of sex in the Hymenoptera and concluded that the number of eggs fertilized (and hence the sex ratio) is influenced by the size of the host in some species, and by the rate of oviposition in others.

Since these factors have been found to influence the sex ratio of certain Hymenoptera, an investigation was conducted to determine whether external factors influence the sex ratio of *A. medicaginis*. When adult *Apanteles* were collected by sweeping various habitats, there was a great variation in the sex ratio. A similar variation, depending on the habitat samples, was observed by Ford (1943). He found that general sweeping yielded a preponderance of males, whereas sweeping combined with a knowledge of the breeding habits of any one species would yield many more females. In the case of *A. medicaginis* it was found that alfalfa fields which had *Apanteles* emerging from them always contained a high proportion of males, whereas fields which contained many parasitizable *Colias* larvae usually had a high proportion of females. In addition, plants which provide

food for adults, such as aphid-infested Johnsongrass (*Holcus halepensis* L.) and sunflowers (*Helianthus annuus* L.), always had an extremely high proportion of males. In a sample of 814 *Apanteles* adults collected on Johnsongrass, females accounted for only 9.6 per cent.

This great variation in the sex ratio from field to field and habitat to habitat can be explained by the different requirements of the two sexes. The males emerge slightly earlier than the females and, as in the case of *Colias eurytheme* (Smith, *et al.*, 1949), the females, after mating, concentrate in fields that contain favorable hosts. The males, on the other hand, tend to remain where females are emerging or seek out habitats which supply adequate food.

TABLE 12

COMPARISON OF SEX RATIOS OF *APANTELES MEDICAGINIS* EMERGING FROM *COLIAS* LARVAE COLLECTED IN FIELDS WITH VARIOUS HOST DENSITIES

Colias density	Number of *Apanteles* examined	Number of females
larvae/sweep		*per cent*
0–0.9	177	50.8
1–1.9	129	51.9
2–4.9	514	43.6
5–10	395	54.2
11–50	624	46.8
50–120	350	53.7

Because of this great variation, it is very difficult to determine the true sex ratio by collecting adults in the field. Sampling of all types of habitats should minimize the effect of habitat preference. When this was done for *A. medicaginis,* the sex ratio was 51.8 per cent females, based on 4,269 individuals.

In order to obtain a more accurate indication of the sex ratio, parasitized larvae were collected, and the parasites were reared to the adult stage. It was then possible to compare the resulting sex ratios with the population density, with the percentage parasitism, and with the host instar from which the parasite larvae emerged. Because oviposition by *Apanteles* in all but the late part of the first instar of *Colias* resulted in emergence from the third instar, and oviposition in the late first, second, and third instar resulted in emergence from the fourth instar, it was possible to determine whether oviposition had been in small or relatively large *Colias* larvae.

Field collections in various areas showed that population density of *Colias* did not affect the sex ratio (table 12). Since fields with high host populations should increase the rate of oviposition of *Apanteles*, it would be logical that, if the rate of oviposition influenced the sex ratio, there should be a correlation with the host density. This does not seem to be the case, however, for there is no correlation between the sex ratio and the host density.

Laboratory observations on the oviposition habits of *A. medicaginis* help to explain why host density does not affect the percentage of eggs ferti-

lized. In those species of insects that are affected, increased density increases the rate of oviposition which, in turn, results in a decrease in the number of eggs fertilized. In the case of *A. medicaginis,* however, continued availability of hosts does not result in a very high rate of oviposition. The behavior of females after oviposition indicates that considerable time must elapse before another egg can be laid. After oviposition the females manipulate their abdomens violently and then remain inactive for a short period of time before they can be stimulated to oviposit again.

There is no correlation between the sex ratio and the percentage parasitism in a field (table 13). If one sex were intrinsically superior to another,

TABLE 13

COMPARISON OF SEX RATIOS OF *APANTELES MEDICAGINIS* EMERGING FROM LARVAE COLLECTED IN FIELDS WITH VARIOUS DEGREES OF PARASITISM

Colias parasitized	Number of *Apanteles* examined	Number of females
per cent		*per cent*
0–9	111	49.5
10–19	35	45.7
20–29	33	63.6
30–39	65	63.1
40–49	55	43.6
50–59	404	54.2
60–69	221	54.3
70–79	158	55.1
80–89	121	55.4
90–100	986	43.2

and if superparasitism were of common occurrence, the sex ratio could probably be correlated with changes in the degree of parasitism. However, since superparasitism does not seem to be of common occurrence, it is unlikely that the percentage of the hosts parasitized would influence the sex ratio.

The size of the host at the time of parasitism likewise does not seem to influence the sex ratio. Females constituted 50.3 per cent of 1,490 individuals emerging from the third instar, and 62.1 per cent of 214 reared from the fourth instar. This might suggest that parasitization of larger *Colias* larvae results in a higher proportion of females. However, little weight can be placed on these observations because of the large variation in the samples. A chi square analysis of the data, based on the hypothesis that the sex ratio of those emerging from the fourth instar would be 50 per cent females, showed that the ratio was significantly different from 50 per cent, but an analysis of variance between those emerging from the third and fourth instars showed no significant differences.

Since environmental factors do not seem to influence the sex ratio of parasites actually emerging, an over-all sex ratio was calculated for all the adults reared from various field samples. The ratio obtained was 51.0 per

cent females, based on 2,937 individuals. This agrees very closely with 51.8 per cent females obtained by sweeping adults from alfalfa fields.

These figures are in close agreement with the sex ratios found for other *Apanteles* by various workers. Ford (1943) found that in numerous solitary *Apanteles,* the sexes were about equal, and gregarious species had a preponderance of males. Richards (1940), working on *Apanteles rubecula* Marshall, a solitary parasite of *Pieris rapae,* found that the sex ratio was 1.0 female:0.9 male, or 52.6 per cent females. It would seem that *A. medicaginis,* like other solitary *Apanteles,* has a sex ratio of about 50 per cent females, and that environmental conditions have little effect on this ratio. Since environmental conditions do not tend to increase the proportion of males in *A. medicaginis,* the sex ratio does not adversely influence the effectiveness of this parasite.

HYPERPARASITISM

Hyperparasitism, or secondary parasitism, is often an important factor affecting the efficiency of a parasite (Proper, 1934; Sweetman, 1936). Many *Apanteles* seem very susceptible to attack by hyperparasites (Muesebeck and Dohanian, 1927). In his comprehensive study of the hyperparasites of *Apanteles glomeratus,* Blunck (1950, 1951*a*, 1951*b*, 1952*a*, 1952*b*) found an extensive fauna living at the expense of this parasite; however, *A. medicaginis* does not seem to be nearly so heavily attacked by hyperparasites.

In order to study the effect of hyperparasites, *Apanteles* cocoons were collected in various fields and brought into the laboratory. These cocoons were held until all *Apanteles* and hyperparasites had emerged, after which the percentage hyperparasitism was calcuated on the number of cocoons collected. Because large numbers of cocoons were necessary for this study, they were collected in fields which had very high *Apanteles* populations. Although hyperparasites are not specific in their attack, they should act in a density-dependent manner; thus, fields with high *Apanteles* populations should have the maximum amount of hyperparasitism.

The amount of hyperparasitism in the eight fields examined averaged 5.1 per cent (table 14). The exceptionally high hyperparasitism of 18.1 per

TABLE 14

HYPERPARASITISM OF *APANTELES MEDICAGINIS*

Locality	Date	Number of cocoons	Hyperparasitism			
			Catolaccus aeneoviridis	*Spilochalcis side*	*Eupteromalus viridescens*	Total
			per cent	*per cent*	*per cent*	*per cent*
6 mi. S.E. of Dos Palos	Aug. 15, 1949	128	3.9	3.1	0.0	7.0
7 mi. E. of Dos Palos	Aug. 28, 1949	152	2.6	0.7	0.7	3.9
7 mi. E. of Dos Palos	Aug. 31, 1949	66	0.0	1.7	0.0	1.7
7 mi. E. of Dos Palos	Sept. 1, 1949	154	1.9	0.0	0.0	1.9
3 mi. S. of Dos Palos	Oct. 6, 1949	99	18.1	0.0	0.0	18.1
7 mi. E. of Dos Palos	July 24, 1950	167	3.6	1.2	0.0	4.8
6 mi. S.E. of Dos Palos	Aug. 24, 1950	134	0.0	0.8	0.0	0.8
6 mi. S.E. of Dos Palos	Sept. 7, 1950	465	3.7	0.7	0.0	4.4
Mean			4.0	1.0	0.1	5.1

cent in the one field, which added appreciably to the mean value, can probably be explained by two factors. First, this collection was made late in the season, and second, the field from which the sample was collected was one of a group of fields that were cut after a very long growing period.

Catolaccus aeneoviridis (Girault), a pteromalid, was by far the most important hyperparasite in the Dos Palos area. In the fields sampled, this species parasitized 4 per cent of the *Apanteles* cocoons, whereas *Spilochalcis side* (Walker) parasitized 1 per cent, and *Eupteromalus viridescens* (Walsh) was reared from only one *Apanteles* cocoon. The latter two species are rather general in their attack, and have been reported on several other *Apanteles* species (Balduf, 1929; Vickery, 1929; Muesebeck *et al.*, 1951). Although a limited number of fields were sampled for quantitative data on hyperparasitism, numerous cocoons were collected from other fields, and in all cases the species involved and the proportions were similar to the data in table 14. Although *Catolaccus* can destroy *Apanteles* by adult feeding as well as by actual parasitism, it does not appear that hyperparasites play an important role in limiting the efficiency of *A. medicaginis*. Cocoons which had neither *Apanteles* nor hyperparasites emerging from them might indicate an effect of adult hyperparasites feeding on pupae within the cocoons; however, in most cases the number of cocoons that had no emergence from them was relatively low, and there was no correlation between *Catolaccus* density and unexplained mortality.

A brief study was made of the biology of *Catolaccus aeneoviridis* (Girault), the most abundant hyperparasite. Its habits were found to be similar to those of *Habrocytus cerealellae* (Ashmead), a parasite of the Angoumois grain moth, *Sitotroga cerealella* (Olivier) (Noble, 1932; Fulton, 1933).

Catolaccus aeneoviridis is a pteromalid which Girault (1911) described as *Arthrolytus aeneoviridis* from Iowa. Subsequent to its description it has been recorded on many hosts, including several *Apanteles,* and Vickery (1929) discussed the biology of this species (as *Dibrachys meteori* Gahan).

In order to study the biology of this hyperparasite with *A. medicaginis* as its host, adults were placed in pint-sized ice cream cartons which were covered with petri dishes. The adults were fed honey and raisins, and newly spun cocoons of *Apanteles* were placed in the containers for parasitization. These cocoons were removed after parasitization, and were either dissected or reared at 26.7° C, depending on the information desired.

When recently-emerged males and females were brought together, mating took place readily. Upon coming into contact with females, the males vibrate their wings rapidly and then jump upon the back of the female. The male advances to the mesonotum of the female and moves his antennae in front of the female. The male then moves back on to the abdomen of the female and inserts the tip of his abdomen into the genital aperture of the female. Actual sexual contact occurs for only a few seconds.

When supplied with food, *Catolaccus* adults lived a long time as contrasted with *Apanteles*. Although precise data are not available, the longevity of *Catolaccus* would seem comparable with that of *Habrocytus*, which Noble (1932) determined to be 41.14 days for females and 31.84 days for males, at 24° to 25° C.

The preoviposition period is about two days. Females are readily attracted to *Apanteles* cocoons, but show no interest when larvae are not present in the cocoon. On coming into contact with a cocoon, a female inspects it with her antennae and then pierces it with her ovipositor. The ovipositor is used in an exploratory manner until contact is made with the host larva within, and then the female paralyzes the host. After paralysis of the host, the action of the female is dependent on whether she is stimulated to feed or to oviposit.

In order to feed on the *Apanteles* larva, the female must construct a feeding tube. This she does by inserting her ovipositor into the cocoon and secreting a clear fluid which flows down the sheath of the ovipositor. Construction of this tube extending from the host larva to the outside of the cocoon requires about four minutes. During most of this time the ovipositor is manipulated up and down. Upon completion of the feeding tube the ovipositor is removed and the female laps up the host fluids which rise in the tube. Feeding may extend over a period of 15 minutes.

Oviposition often occurs in hosts which have been fed on previously. This operation requires a much shorter time than construction of a feeding tube. The egg, which is very large, passes down the ovipositor by constriction, like sand in an hour glass (Fulton, 1933). A single egg is deposited by a female and, in all cases observed, eggs were deposited on hosts which had not advanced to the pupal stage, although Vickery (1929) stated that this species would oviposit on individuals in the pupal stage. Females show no discrimination between parasitized and unparasitized cocoons, so that when females are enclosed with a limited number of cocoons, each cocoon receives a large number of eggs. Although numerous eggs may be laid on each host larva, only one completes its development. Upon hatching, the larvae destroy all the eggs encountered within a cocoon, and when two larvae come into contact, one is always destroyed. In addition to this internecine action, it was found that, in cocoons which contained numerous eggs, many were collapsed before any larvae had hatched. This suggests that the adult, through probing of the ovipositor, destroys many previously deposited eggs.

Developmental time at 26.7° C averages about 14.75 days, with the males requiring a slightly shorter time than the females. The egg stage requires between one and two days, the larval stage about seven days, and the pupal stage about six days.

Information on the biology of *Catolaccus aeneoviridis* helps explain why this hyperparasite is not more abundant on *A. medicaginis*. The fact that the developmental time of *C. aeneoviridis* is 14 days at 26.7° C indicates that the cutting of alfalfa is detrimental to this hyperparasite. At 26.7° C, *Colias philodice eurytheme* requires 24 days for development, but to evaluate the time of development for *C. aeneoviridis*, one must take into account the time required for hatching of the *Colias* egg and for larval development of the *Apanteles*. This time amounts to about 15 days which, when added to 14 days for *Catolaccus* development, shows that the time required is 29 days. Since *Colias* emergence is usually closely correlated with cutting of the alfalfa, it can be seen that the longer time required by *Catolaccus*

would generally preclude its emergence before cutting. The temperatures to which cocoons are exposed when the hay is cut in the Dos Palos area during the summer have been shown to be lethal for *A. medicaginis,* and this is probably true for *C. aeneoviridis.*

Another factor in the biology of *C. aeneoviridis* which reduces its efficiency as a hyperparasite is the short period during which *Apanteles* are suitable for attack. *A. medicaginis* spends five days within its cocoon at 26.7° C, but only about one and one-half days of this time are spent as a larva. Since *C. aeneoviridis* does not seem to prefer the *Apanteles* after pupation, only about one third of the cocoons encountered will be suitable for attack. This short period of suitability of the host, plus a limited searching capacity of the hyperparasite, undoubtedly limits the detrimental effect of the latter on *A. medicaginis.*

The low hyperparasitism can also be explained by the biology of *A. medicaginis.* Most other species of *Apanteles* that are severely attacked by hyperparasites overwinter as cocoons and thus are subject to a prolonged period of attack. This is true for both *A. melanoscelus* Ratzeburg (Muesebeck and Dohanian, 1927) and *A. glomeratus* Linn. (Farwick, 1947), but *A. medicaginis* overwinters as an immature larva inside its host and thus avoids attack. It is true that certain hyperparasites of *Apanteles,* such as *Tetrastichus,* attack the *Apanteles* within the host larvae (Martelli, 1907; Gautier and Bonnamour, 1924; Blunck, 1944) but none of these has been found on *A. medicaginis.*

INTERFIELD MOVEMENTS

Since alfalfa is cut periodically, it is important to understand the effect of this cutting on *Apanteles* adults. Cutting, which removes practically all surface vegetation, changes the habitat drastically and thus produces a very critical period for *Apanteles* survival. If alfalfa is cut early in the pre-bud stage of maturity, some green foliage remains on the stems. If cut at the proper time of about 1/10 bloom, almost no green growth remains in the alfalfa field. If cut later, then new shoots have started to appear. The importance of cutting on *Colias* populations has been demonstrated by the work of Smith *et al.* (1949). In addition, laboratory evidence suggests that *Apanteles* adults must either move out of fields when they are cut or be killed by the adverse conditions following cutting.

During the course of this work, a study was made of the movement of adult *Apanteles* at the time of cutting. The first method of sampling populations was the use of "sticky boards" similar to those used by Kaloostian and Yeomans (1944) in pear psylla studies. These consisted of plywood boards (5 × 10 inches) painted various colors and coated with a thin layer of tanglefoot ("Deadline," manufactured by the California Spray Chemical Corporation). These sticky boards were placed in alfalfa fields known to contain adult *Apanteles.* The boards were attached to steel poles in such a manner that they could be oriented in various positions with regard to the alfalfa and wind.

It was soon found that very high populations were necessary to obtain adequate numbers of adults on the boards. The color of the boards had no

effect on their attractiveness, but their positions with respect to the alfalfa did have a marked influence on the numbers captured. This is not surprising, for adults usually fly below the tops of the alfalfa plants, and it was in this area that the greatest numbers were obtained. However, even these numbers were not an adequate sample. In certain fields with extremely high populations of *Apanteles*, large numbers of individuals appeared on the boards (a maximum of 260 on one side), but in fields with lower populations the numbers were not large enough to evaluate quantitatively.

Subsequent work showed that sweeping the top few inches of alfalfa with an insect net gave a much more reliable indication of the adult population. Sampling the same fields by the two methods showed that a population represented by 30 adults per 50 sweeps with an insect net would yield only about two individuals per day on a sticky board. Because of this low recovery the use of sticky boards was abandoned.

The 50 sweeps used to sample the population were made with a net similar to the University of California standard insect net (Smith and Smith, 1951) except that the net bag was made of marquisette. Sweeps were made in a manner similar to those described by Linsley (1945, 1946). The end of the net handle was held in one hand, and the arm was extended to sweep the net over the top few inches of the alfalfa in an arc of 180 degrees. The penetration of the net into the alfalfa varied somewhat, but was approximately 2 inches. In fields with extremely high larval populations this had the disadvantage of gathering numerous caterpillars in the net, but separation of the adults, although difficult, was still possible. In stubble fields the sweep was modified so that the net passed just over the top of the stubble.

After the 50 sweeps were made, the entire contents of the net were placed in a gallon cyanide jar until the *Apanteles* were dead. The *Apanteles* were then removed from the other material and stored until they could be counted and their sex could be determined in the laboratory.

In studying interfield movement, a group of five fields comprising 900 acres was selected. These fields, situated about 6 miles east of Dos Palos, are designated as the Harmon area for convenience. They were chosen because they were more or less isolated from other alfalfa and were in an area that usually had high populations of *Apanteles*. The fields (fig. 5) were bordered on the east by the San Joaquin River, on the north and west by cotton, and on the south by cotton and alfalfa. Fifty-sweep samples were taken at various positions in the fields so that population trends could be followed.

Sampling by the sweep method was not found to be feasible until August 8; hence only a few fields were sampled during the first phase of this study. However, the data (table 15) indicate the general picture in this area. Field C was in the emergence stage at the start of the study. Samples taken in this field on August 8 and 9 gave a relatively high proportion of males and suggested that females had moved out prior to cutting. This field was cut on August 10, and samples taken on August 10 and 11 revealed that the female population was very low. Samples taken at this time in fields B and E suggest a movement down wind into field E from field C. This observation was substantiated by the presence of considerable numbers of *Apan-*

TABLE 15

TRENDS OF POPULATIONS OF ADULT *APANTELES MEDICAGINIS* IN ALFALFA IN THE HARMON AREA, 1949

Date	Field A			Field B			Field C			Field D			Field E			Field F		
	Stage of growth	*Apanteles* per 50 sweeps		Stage of growth	*Apanteles* per 50 sweeps		Stage of growth	*Apanteles* per 50 sweeps		Stage of growth	*Apanteles* per 50 sweeps		Stage of growth	*Apanteles* per 50 sweeps		*Stage* of growth	*Apanteles* per 50 sweeps	
		males	*females*		*males*	*females*		*males*	*females*		*males*	*females*		*males*	*females*		*males*	*females*
8/8	....	..	..	..	..	..	....	11	7.5	....	..	..	....	..	..	..	..	..
8/9	....	..	..	..	0.5	4	....	15.5	4	....	..	..	....	..	..	..	..	..
8/10	....	..	..	¼	1	6	cut	12.5	0.5	....	..	..	....	0	5	..	..	..
8/11	....	..	..	..	3	5	....	12	1	....	..	..	....	2	15	..	..	..
8/15	....	..	..	½	2	33	....	7.5	1.5	....	..	..	¾	1.5	16.5	..	..	..
8/16	¾	3	10	..	2	28	....	8	3	cut	28	23	....	13	20.5	..	2	29
8/17	....	32	37	..	2	26	stubble	5.5	0.5	....	1	1	....	10	26	..	..	..
8/24	cut	..	..	..	6	14	first leaves	0	7	....	..	..	cut	2	0	..	..	..
8/25	....	2	0	..	3.5	10	....	0	10	first leaves	4	2	....	4	0	¾	18	31
8/26	....	..	..	..	0.5	5.5	....	..	..	....	..	..	....	..	..	..	..	..
8/30	first leaves	1	1	¾–full	60	11	¼	0	6	....	0	0	....	6	2	..	..	..
8/31	....	2	6	..	189	14	....	0	6	....	6	6	....	8	2	cut	84	0
9/1	....	5	8	cut	9	0	....	12	22.5	....	5	16	....	10	5	..	..	..
9/7	¼	3	12	..	22	6	½–¾	18	30	¼–½	2	17	first leaves	11.5	20	..	..	..
9/8	....	..	..	..	..	..	....	26	32	....	..	..	....	..	..	..	..	..

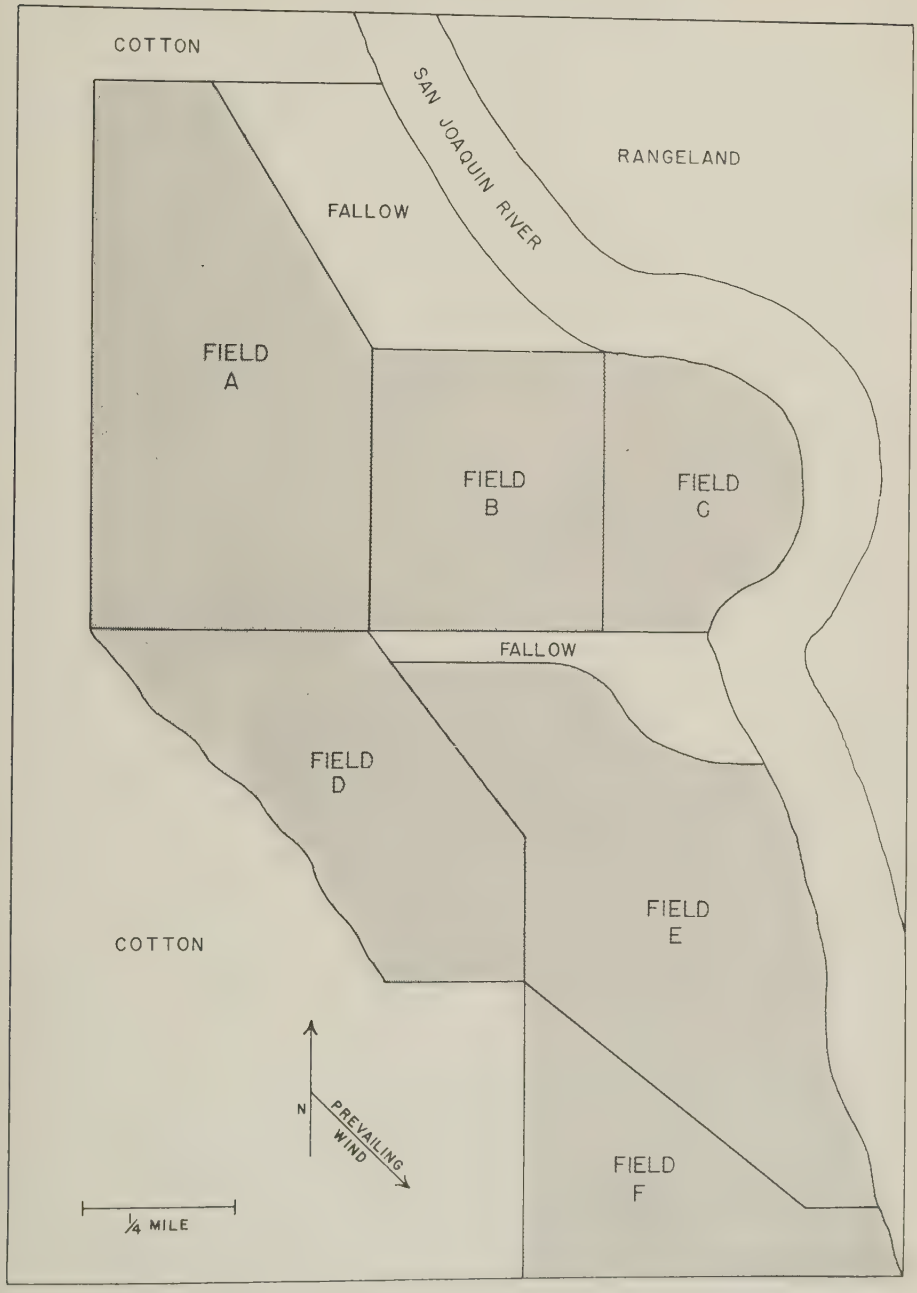

Fig. 5. Map of the Harmon experimental area. The shaded areas indicate alfalfa fields.

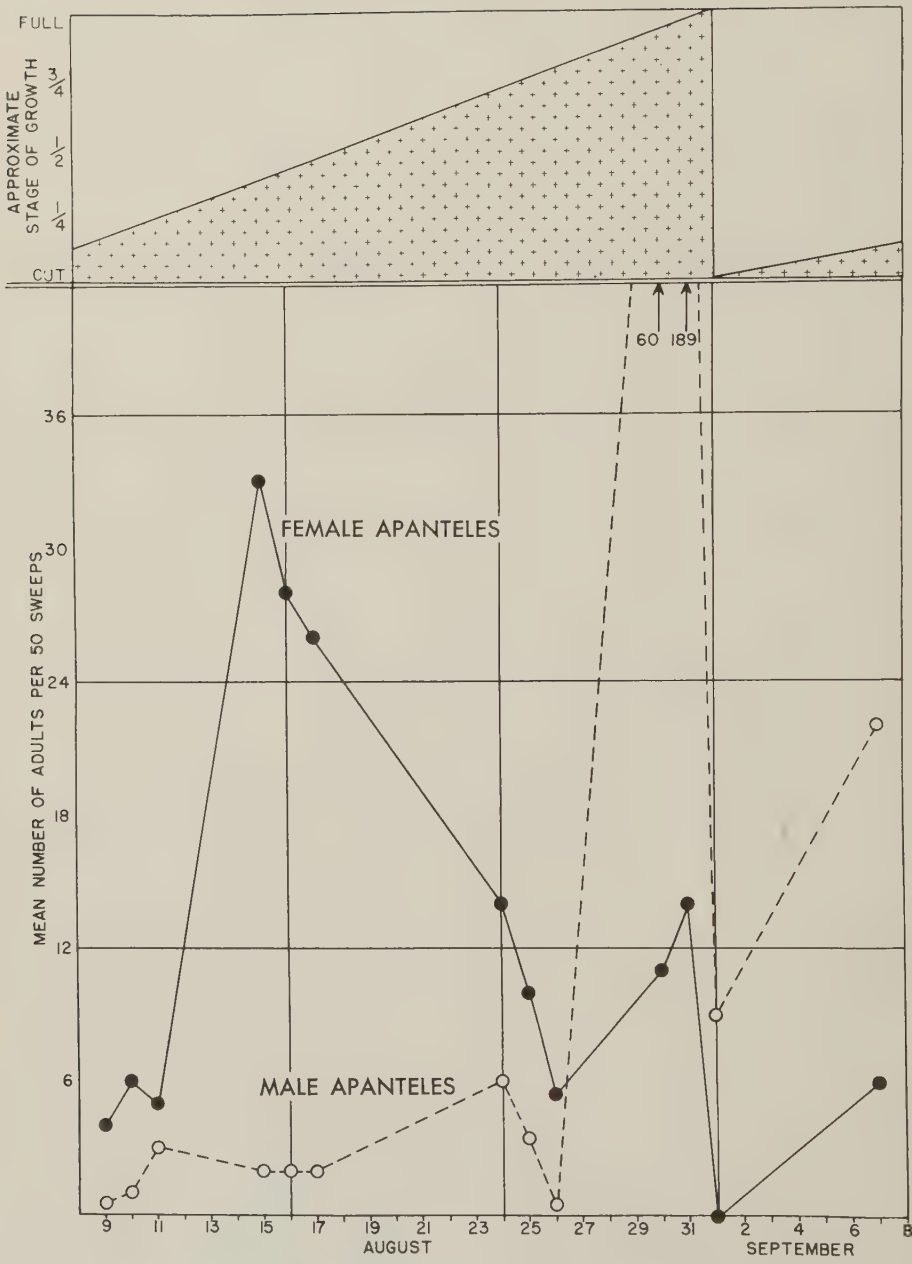

Fig. 6. Population trends of male and female *Apanteles* (below) in an individual alfalfa field correlated with the stage of growth of the alfalfa (above).

teles in a strip of Johnsongrass (*Holcus halepensis* L.) connecting fields C and E. Although samples were not taken in field D at the time, it is probable that a similar migration into that field took place.

When sampled on August 9, field C yielded 15.5 males and four females. On the following day, when this field was cut, the adjacent Johnsongrass yielded 114 males and only four females. It thus seems probable that males move to surrounding vegetation on which they can feed, while the females continue in search of a habitat where suitable hosts may be found.

Population samples were again taken on August 15 and 16. At that time, field B showed a great increase in the numbers of female *Apanteles*. The presence of numerous small *Colias* larvae in the field probably explains the numbers of female *Apanteles*. The lack of appreciable numbers of parasitized *Colias* larvae in surrounding fields at that time precludes emergence as an explanation. It would appear that the movement of *Apanteles* females produced an "effective concentration" as in the case of *Colias* (Smith *et al.*, 1949). Miyashita (1956), studying *A. glomeratus*, did not find such a concentration where hosts were present. However, populations of *Pieris* would not be so markedly different as those encountered with *Colias* on alfalfa.

On August 16 and 17 field D was cut. This field was cut from south to north, and it showed a pronounced drop of *Apanteles* in the part that was cut, and considerable concentration of adults in the uncut hay adjacent to the cut portion. Sweeps made when half the field was cut yielded no individuals in 50 sweeps at the south end where the alfalfa had been cut six hours earlier. The north end, which was farthest from the cut portion, yielded 13 males and 20 females in 50 sweeps. The alfalfa in the center of the field adjacent to the cut alfalfa yielded 136 males and 95 females per 50 sweeps. This could only be accounted for by movement and concentration. It is therefore not surprising that field A showed a pronounced rise in its adult population. Field E, adjacent to field D, likewise showed an increase, but not nearly so pronounced. This suggests that the direction in which the field is cut also affects the direction of movement.

The next population samples were taken on August 24, 25, and 26. In the week prior to these counts, field A was cut on August 18 and field E was cut on August 22. The samples indicate that nearly all the adults had disappeared from both the fields that were cut. Samples from the other fields at this time showed a slight rise in fields C and D. The greatest number of females were found in field F, but even here there was little rise over the previous week's count. At this time adult populations seemed to be at a minimum as a result either of death or of movement into fields south of F. Field F had a very high *Apanteles* population in the *Colias* larvae. The alfalfa was cut too early for all of the *Apanteles* to complete development but, nevertheless, the emergence was high. Samples on August 30 and 31 in fields D and E, adjoining field F on the north, did not show any appreciable increase in adult *Apanteles*. The sex ratio of the *Apanteles* in field F on August 31, and the lack of *Apanteles* in the adjacent fields to the north once again indicated movement was down wind.

Samples taken in Field B on August 30 and 31 indicate that there was a sizeable emergence from this field. Once again the males greatly exceeded the females, and samples taken in fields A and D indicate that the females dispersed before the fields were cut. It was not determined whether the

females seek out new growth, where small larvae are most likely to occur, or merely continue to move until suitable hosts are encountered.

On September 1, field B was cut, with a resulting drop in the adult population. Counts in the other fields at this time showed a general population increase which was most pronounced in fields C and D. Since none of the other fields could have had adults emerging from them at that time, it is likely that the rise in population was a result of movement from field B. A final count on September 7 substantiated this general rise in population. By that date, emergence seemed to have started from field C because, on September 8, the number of males was increasing.

Figure 6 shows the change in the sex ratio of the adults in field B. On August 9, that field had recently been irrigated and the first leaves were starting to grow. Oviposition by *Colias* over the ensuing week was heavy, resulting in a large larval population. The female *Apanteles* population was highest on August 15. These females were undoubtedly concentrated in this field because of the numerous small *Colias* larvae present. The population of males at the same time remained at a low level. The period August 19 to 26 was characterized by a general decrease in the *Apanteles* females. This can most probably be explained by the decreasing number of parasitizable larvae present and by mortality of the females. From August 26 until the field was cut on September 1, there was a slight increase in females and a very large increase in males. This change in the population is most readily explained by emergence. The males remained in the field to mate with the emerging females, whereas the females, after mating, sought out habitats where parasitizable larvae were present.

This study on the interfield movement of *Apanteles medicaginis* shows how populations of the adults can be followed. It was found that populations of both males and females vary greatly according to the stage of growth of the alfalfa. In fields where *Apanteles* are emerging, the males always greatly outnumber the females. This is partially the result of males emerging first. Of greater importance, however, is the fact that the males tend to remain in the field of emergence, whereas the females move to other areas. When fields are cut, the marked changes in the habitat cause both the males and females to leave the stubble field. When forced from a field that has been cut, the males tend to concentrate in habitats which provide food for the adults. Females, on the other hand, tend to concentrate in fields which contain parasitizable larvae. Since *Apanteles* adults and *Colias* butterflies differ in their ability to fly from field to field, they are often concentrated in different fields after cutting. This separation of host and parasite populations after cutting is another factor limiting the effectiveness of *A. medicaginis*.

SUMMARY

Investigations were conducted to determine the more important factors influencing the efficiency of *Apanteles medicaginis* as a parasite of *Colias philodice eurytheme*. Studies on the developmental rates of *Colias* at various temperatures show that high temperatures are essential for this insect to be of economic importance. At low temperatures the time of development exceeds the time normally encountered between cuttings of alfalfa, and

populations never develop to economic proportions. It is only in areas with moderately high temperatures that *A. medicaginis* becomes an important factor in the control of *C. ph. eurytheme*. *A. medicaginis*, which requires a much shorter time for development, should be able to respond rapidly to changes in host density. However, this ability to respond rapidly is limited by the changes in the habitat produced by cutting of the alfalfa. Cutting causes *Colias* populations to be relatively even-brooded in any particular field, and also necessitates periodic movement of host and parasite populations at the time of each cutting.

Because *Colias* larvae in any particular field are more or less in the same stage of development, and because alfalfa is cut about every 30 to 35 days, it is very difficult for *A. medicaginis* to complete two generations in a field between cuttings. Consequently, the *Apanteles* females emerging from a field must either seek out another population of *Colias* in a parasitizable stage or wait for the emergence and resulting progeny of the *Colias* from the same field. This difference in the time of emergence, coupled with the difference in flight characteristics and host habitat selection, at times may result in concentrations of hosts and parasites in different fields. This separation of the two populations leads to circumstances whereby a large number of *Apanteles* may be available to attack a small number of *Colias* or, on the other hand, a small number of *Apanteles* females must at times cope with very large numbers of *Colias* larvae to effect control. Under the latter circumstances, limited longevity and associated low reproductive capacity are important factors limiting the efficiency of *A. medicaginis*. In substantiation of this hypothesis, areas which contain many sources of food for adult *Apanteles*, thus favoring increased longevity, generally have a higher degree of parasitism.

A. medicaginis exhibits little discrimination between parasitized and nonparasitized hosts under crowded conditions in the laboratory. However, this does not hold true in the field. Dissection of numerous field-collected *Colias* larvae indicates that superparasitism is very low and is not an important factor limiting the efficiency of *A. medicaginis*. Like many other solitary *Apanteles*, this species has a 1:1 sex ratio, and environmental conditions normally encountered in the field have little influence on this ratio. Hyperparasitism, which at times can be an important factor limiting the efficiency of a parasite, seems of little importance in the case of *A. medicaginis*. This is explained by the lack of opportunities for the hyperparasites to attack *A. medicaginis* and the adverse effect that cutting of alfalfa has on development of the hyperparasites.

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